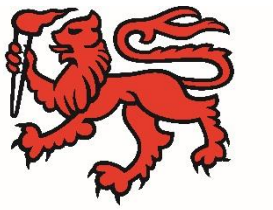

DEMOGRAPHY OF TWO SYMPATRIC FUR SEALS (*Arctocephalus gazella* and *Arctocephalus tropicalis*): INTRINSIC AND EXTRINSIC DETERMINANTS OF SURVIVAL

Submitted by

Debbie Emma Baird-Bower

B.Sc. (Queen's University Belfast) and M.Res. (Swansea University)

Institute for Marine and Antarctic Studies

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Declaration and Statements

Declaration of Originality

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Debbie E. Baird-Bower September 2020

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Abstract

Population ecology is key to understanding a population's behaviour over time, and is important in the development of population viability analysis. To develop robust and accurate population survival estimates, an understanding of the intrinsic (density-regulating) and extrinsic (environmental) factors determining individual survival rates is needed. Here a unique 26-year capture-mark-recapture study on two sympatric fur seal species, Antarctic fur seal (*Arctocephalus gazella*) and subantarctic fur seal (*Arctocephalus tropicalis*) from Macquarie Island, was used to quantify demographic responses of animals to intrinsic and extrinsic factors.

Quantifying survival rates requires individuals within a population to be identifiable and monitored throughout their lives. However, *A. gazella* and *A. tropicalis* have no easily identifiable natural markings, therefore individuals need to be marked with an individually numbered plastic flipper tag. Despite their utility in demographic studies, flipper tags can be lost during an animal's lifetime leading to under-estimates of individual survival. Consequently, estimating tag loss is a central component of estimating survival rates; if the tag loss rate is underestimated the survival rate is negatively biased and *vice-versa*. All seals were tagged with at least two tags, one in each flipper, and some with a sub-cutaneous radio-frequency identification tag as a form of long-term identification, allowing dependent tag loss rates to be calculated. Using a Bayesian approach these data were analysed to quantify the rate of tag loss. Tag loss was age-dependant, with pups having a higher probability (0.4 (95% credible interval: 0.19, 0.58)) than juveniles (0.08 (0.005, 0.23)) and adults (0.04 (0.008, 0.08)) of losing both tags. There was little evidence for differences in the tag loss rates between the sexes and species. The tag loss estimates from this study provided an opportunity to accurately quantify how survival is affecting population growth rates in this unique population that is growing at a substantially lower rate than other similar colonies.

The Macquarie Island fur seal population is unique among other fur seal populations in that three species of fur seal *A. gazella, A. tropicalis,* and New Zealand fur seal (*Arctocephalus forsteri*) occur on the island, and 17-30% of the population have been identified as hybrids of these three species. It has been suggested the slow growth rate of the Macquarie Island fur seal population may be in part due to the high rates of hybridisation between the three species. With genetic profiles from mitochondrial DNA and microsatellites to distinguish

pure species (n = 682) from hybrids (n = 208) hybrid survival probabilities and population growth rates were then compared within a Bayesian framework with those of pure-breed *A. gazella* and *A. tropicalis* to estimate if there was a survival cost associated with hybridisation. Modelling showed hybrids had comparable survival rates to pure-breds of both species throughout all age classes; pups, juveniles and adults. This suggests that the survival cost associated with hybridisation was not a key factor in the population's slow growth (3.4% for *A. tropicalis* and 8.6% for *A. gazella*). Examination of other potential factors which may limit the population growth rate of *A. gazella* and *A. tropicalis* found the populations low numbers and high predation risk from New Zealand sea lions (*Phocarctos hookeri*), in addition to distance from other breeding colonies were key factors in the slow population growth rate.

With these extrinsic (tag loss) and intrinsic (hybridisation) sources of survival bias quantified, the effect of environmental variability on survival was then determined for *A. gazella* and *A. tropicalis*. Despite occupying a similar at-sea niche (having the same prey and foraging behaviour), *A. gazella* and *A. tropicalis* had different survival responses to sea surface temperature, sea level pressure (an indication of the Southern Oscillation Index), and wind speed; which was attributed to differences in life lactation strategy. Adult *A. gazella*, with a lactation period averaging four-months, had a higher survival probability, than *A. tropicalis* with a nine to eleven-month lactation period, during periods of high sea level pressure, warm sea surface temperature, and high wind speed. This suggests *A. gazella's* ability to migrate and forage away from the breeding colony, for eight months of the year, allows them to exploit more highly productive waters further from Macquarie Island and may confer an advantage. The contrasting survival responses of these sympatric species to wind speed, sea level pressure, and sea surface temperature suggest as the Southern Ocean warms the *A. gazella* population at Macquarie Island will continue to increase while *A. tropicalis*, which are listed as endangered within Australia territory, are at risk of population decline over time.

Statement of Publication and Co-authorship

Chapters two, three and four are in preparation for submission to peer-reviewed journals.

The following people and institutes contributed to the publication of the research undertaken as part of this PhD:

Chapter Two Baird-Bower, D. E. (70%), Schwarz, L. K. (15%), Hindell, M. A. (5%), McMahon, C. R. (5%), Goldsworthy, S. D. (5%)

Chapter Three Baird-Bower, D. E. (65%), Schwarz, L. K. (15%), Hindell, M. A. (5%), McMahon, C. R. (5%), Goldsworthy, S. D. (5%), Lancaster, M. L. (5%)

Chapter Four Baird-Bower, D. E. (70%), Schwarz, L. K. (10%), Hindell, M. A. (10%), McMahon, C. R. (5%), Goldsworthy, S. D. (5%)

Details of Authorship

Debbie E. Baird-Bower (University of Tasmania) was lead author on all manuscripts and was responsible for the research design, data analysis and interpretation and preparation of the manuscript.

Mark A. Hindell (University of Tasmania) provide guidance and supervision in all aspects of the PhD and manuscript preparation.

Clive R. McMahon (University of Tasmania) provide guidance and supervision in all aspects of the PhD and manuscript preparation.

Simon D. Goldsworthy (South Australia Research and Development Institute) provide Macquarie Island mark-recapture fur seal program data, guidance and supervision in all aspects of the PhD and manuscript preparation.

Lisa K. Schwarz (University of California) delivered the Metropolis within Gibbs Bayesian program, provided analysis advice and manuscript preparation for Chapters Two and Three.

Melanie L. Lancaster (Healesville Sanctuary) provided genotypes of Macquarie Island put, input into analysis and manuscript preparation for Chapter Three.

We the undersigned agree with the above state "portion of work undertaken" for each of the above manuscripts published or in preparation for submission to peer-reviewed journals contribution to this thesis chapters.

Debbie E. Baird-Bower	Date: 22nd May 2017
Mark. A. Hindell	Date: 23rd May 2017
Clive R. McMahon	Date: 23rd May 2017
Simon D. Goldsworthy	Date: 26th May 2017
Lisa K. Schwarz	Date: 25th May 2017
Melanie L. Lancaster	Date: 25th May 2017

We the undersigned agree with the above state "portion of work undertaken" for each of the above manuscripts published or in preparation for submission to peer-reviewed journals contribution to this thesis chapters.

Mark Hindell	Craig Johnson
Primary Supervisor	Head of School, IMAS
University of Tasmania	University of Tasmania

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List of Abbreviations

ANARE	Australian National Antarctic Research Expeditions
APF	Antarctic Polar Front
BOM	Bureau of Metrology
CI	Credible interval
CJS	Cormack-Jolly Seber
CTAB	Cetyltrimethylammonium bromide
DMSO	Dimethyl sulphoxide
DNA	Deoxyribonucleic acid
ENSO	El Niño-Southern Oscillation
GLS	Global location sensing
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
MTG	Metropolis within Gibbs
NOAA	National Oceanographic and Atmospheric Administration
PCR	Polymerase chain reaction
PI	Posterior interval
RFID	Radio Frequency Identification
RFLP	Fragment length polymorphism
SAM	Southern Annular Mode
SD	Standard deviation
SMART	Specific, measurable, achievable, results-oriented and time-fixed
SOI	Southern Oscillation Index
SSHA	Sea Surface height anomaly
SST	Sea surface temperature

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Finally, and without hesitation, I would like to dedicate this thesis to Glynn Bower.
Your support throughout my life shaped me into the person I am today.

Preface

These structures

Excluding the introductory and discussion chapters, this thesis is presented as a series of self-contained papers that have been submitted for publication in scientific journals or are being prepared for submission, therefore there may be some repetition.

Chapter One is a general introduction which outlines the context of the research and provides a brief background on the history of the Macquarie Island fur seals.

Chapter Two estimates dependant tag loss probabilities using a Bayesian multi-event, multi-state model based on the standard Cormack-Jolly Seber (CJS) mark-recapture model. Probabilities of moving from one-tag state to another (*e.g.* the probability of going from two tags to no tags within a year) were calculated at different age-specifics. These analyses were used in subsequent demographic analysis.

Chapter Three examines potential factors that may limit the population growth of the Macquarie Island populations. More specially, utilising genetic profiles from mitochondrial DNA and microsatellites to distinguish pure species from hybrids the survival costs associated with hybridisation is quantified to evaluate if hybridisation is a contributing factor in the slow recovery of the populations.

Chapter Four combines oceanographic and meteorological data with survival rates of *Arctocephalus gazella* and *A. tropicalis* to quantify their survival responses to environmental variability. Furthermore, the survival responses of the two sympatric species provide insight into how life history traits influence a species survival responses to changing environmental conditions.

Chapter Five is the discussion and places the research within the framework of meso-predator climate change demographics.

Chapter One

INTRODUCTION

Environmental Variation and Population Demographics

It is increasingly apparent that current climate change is resulting in significant changes to ecosystems and their inhabitants (Sala et al, 2000; Walther *et al.*, 2002; Parmesan, 2006). Of particular concern for biologists is that the current rate of climate change may be greater than the evolutionary capabilities of many species to adapt to the new, emerging properties of their environment (Chown *et al.*, 2010). Consequently, it has been suggested that climate change is the principal force driving many of the plant and animal population declines that are currently occurring (*e.g.* Butchart *et al.*, 2010; Hoffmann and Sgro, 2011; Younger *et al.*, 2016; Clausius *et al.*, 2017). Population declines are especially prevalent at higher latitudes, such as the Southern Ocean, as these regions have the fastest-changing climates (Gille, 2002; Walther *et al.*, 2002; Kovacs *et al.*, 2012; Oosthuizen *et al.*, 2016).

The Southern Ocean has a number of species which are vulnerable to environmental change, but little is known about the possible consequences of this for most of the species. The Southern Ocean is currently undergoing dramatic changes that, although not uniform across regions, are likely to affect Southern Ocean populations, as their ecology is intimately linked with the biotic and abiotic aspects of the marine environment (*e.g.* Oosthuizen *et al.*, 2015; Oosthuizen *et al.*, 2016; Clausius *et al.*, 2017). To predict the nature and the magnitude of ecosystem changes in the Southern Ocean, and the responses of species to environmental change, it is necessary to develop population trajectory and dynamic models incorporating anthropogenic perturbation and environmental cues.

Developing these kinds of models is challenging as it requires demographic (*e.g.* population size and behaviour, survival and fecundity information) and life history (*e.g.* growth, foraging performance, and reproductive success) data (McLaren and Smith, 1985; Eberhardt, 2002; Sibly and Hone, 2002). Such data sets are rare for long-lived Southern Ocean predators, despite the importance of demographic and life history parameters in underpinning the fundamental dynamics of their populations. To predict how changing environmental factors affect individual survival (mediated by prey distribution and abundance) requires models that incorporate long-term mark-recapture studies and environmental information within a single framework. Integrative approaches can provide key insights on how changes in the environment will ultimately influence population dynamics and trends (Figure 1).

Demographic Implications of Differing Life Histories

Understanding a species' fundamental life history traits is a key component in understanding demographic and population dynamics (Stearns, 1976). In the Southern Ocean, species display a wide array of life history strategies, which fall on a continuum from "fast" r-selected traits, like early maturity and low parental care, to "slow" K-selected traits like long lifespans and numerous breeding cycles (Figure 2).

r-selected species, such as Antarctic Krill (*Euphausia superba*), are characterised by their high capacity for rapid population growth and variable population size, which is predominantly limited by a population's maximum reproductive capacity. Typically, r-selected traits support a species ability to rapidly acquire resources and convert them

into offspring, populations with these "fast" life history traits are often associated with variable and/or unpredictable environmental regions (Reznick *et al.*, 2002). However, as changing environmental factors cause demographic variation across most parts of a r-selected species the life cycle, the population dynamics of r-selected species quickly change in response to environmental variation (Saether *et al.*, 2013).

K-selected species, such as Weddell seals (*Leptonychotes weddellii*), are characterised by slow and stable population growth rates, with population sizes being predominantly determined by the carrying capacity of the environment they occupy (Stearns, 1976). Species with "slow" life history traits are dominate in stable and/or predictable environmental regions. Typically, K-selected species have variable juvenile survival rates, low fecundity rates, and stable adult survival rates to buffer against environmental changes (Reznick *et al.*, 2002) resulting in reduced and often delayed population growth rate responses to environmental variation (Saether *et al.*, 2013).

Given life history traits fall on a continuum (Figure 2), species from a common genus may both be classified as having K-selected life history strategies, yet these species may have differing "slow" and "fast" life history traits (e.g. lactation lengths). These differing life history traits can result in differing demographic responses to environmental variation and form the key to quantifying demographic responses to environmental variation.

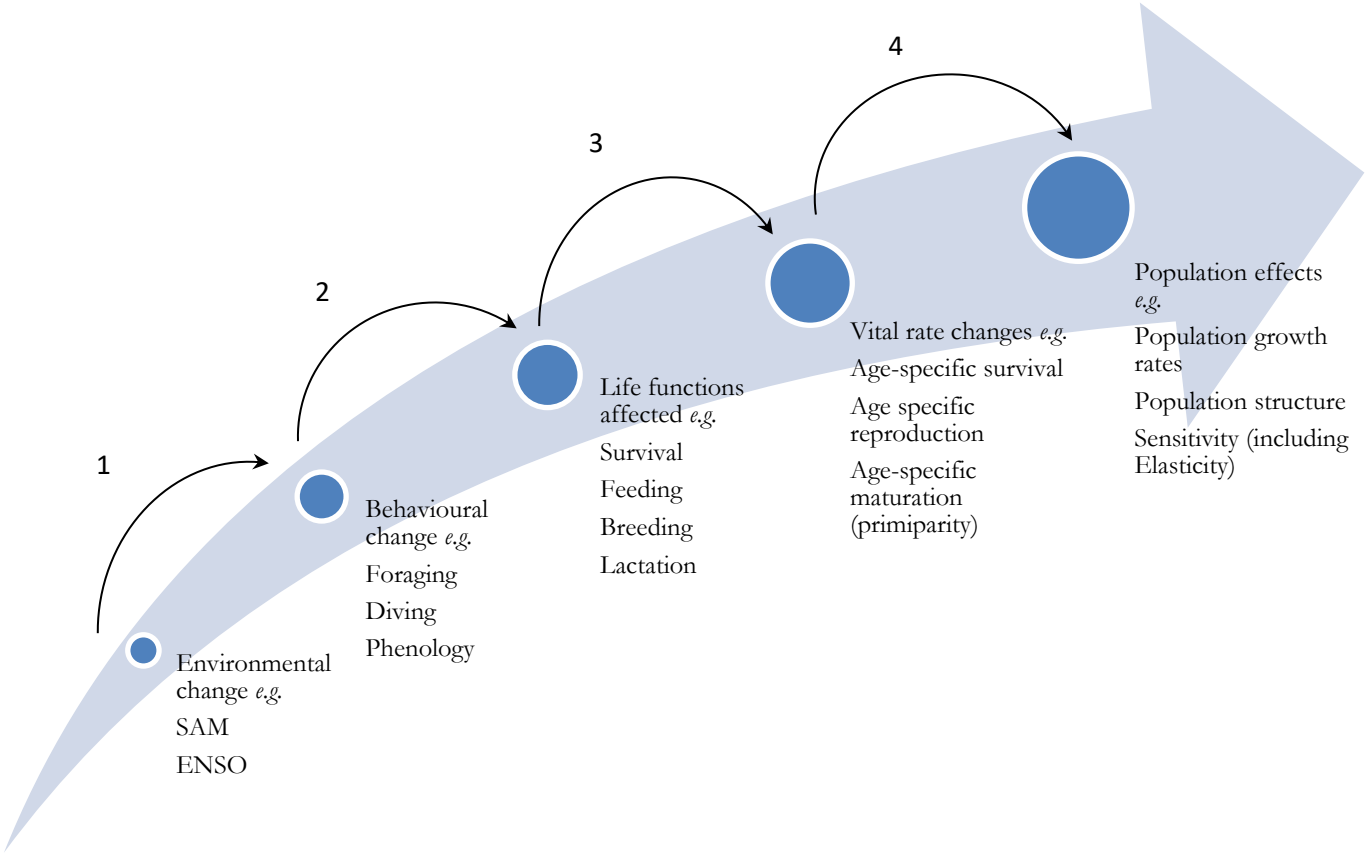


Figure 1. A general conceptual framework of how changes in the environment will effect population performance through several linked stages. Specific transfer functions describe the relationships between the listed variables *e.g.* the relationship between changes in the Southern Annular Mode (SAM) or El Niño Southern Oscillation (ENSO) and foraging behaviour. It is important to note that available knowledge on the relationships between stages is not uniform; it is limited for the relationships described by steps 1, 2 and 3, however, the relationships described by step 4 are well known. Adapted from (New *et al.*, 2014).

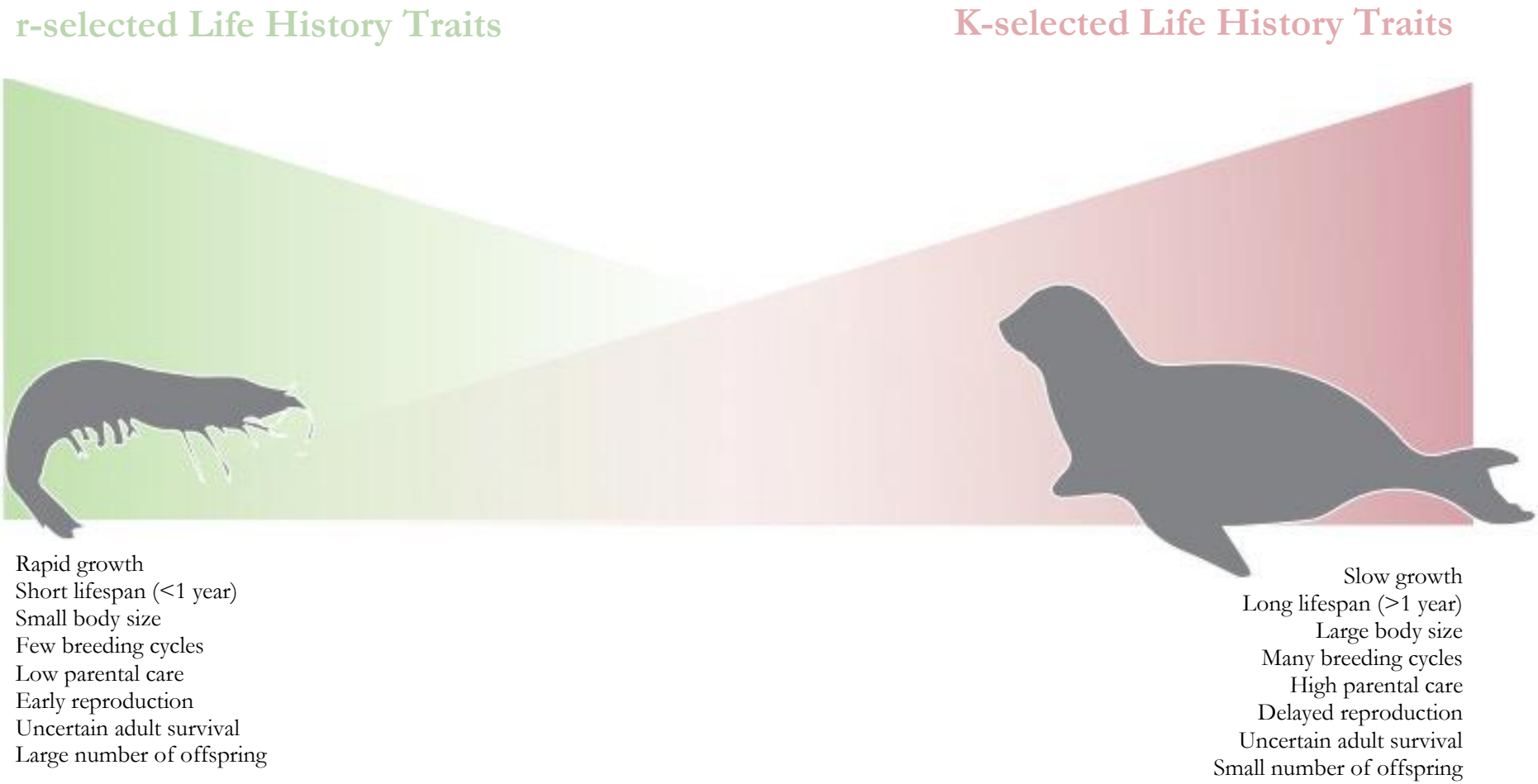


Figure 2. Continuum of (fast) r-selected and (slow) K-selected life history strategies (adapted from Stearns, 1976). Image adapted from Boddy, n.d.

Macquarie Island population

Three meso-predator species occur sympatrically at Macquarie Island: Antarctic fur seals (*Arctocephalus gazella*), subantarctic fur seals (*Arctocephalus tropicalis*), and New Zealand fur seals (*Arctocephalus forsteri*). *Arctocephalus gazella* and *A. tropicalis* have established breeding colonies and constitute the majority of the species' abundance. The majority of *A. forsteri* are transient non-breeding juveniles and adults (Lancaster *et al.*, 2007a; Goldsworthy *et al.*, 2009).

There are several examples of responses of top trophic species to environmental variation. Some migratory species such as birds can migrate earlier in the season, while some fish communities are increasing in abundance in response to warmer sea temperatures, and the foraging distributions of some larger invertebrates are changing (Walther *et al.*, 2002; Grosbois *et al.*, 2008; Pecl *et al.*, 2017). For *A. gazella* and *A. tropicalis* at Macquarie Island there is a strong negative relationship between sea surface temperature and fecundity rates (Goldsworthy and Gales, 2008a), and also a strong negative relationship between sea surface temperature and pup growth (Goldsworthy *et al.*, 2008). However, the relationship between environmental change, other important demographic variables have not been explored.

Understanding the implications of environmentally mediated changes in survival rates on population trajectories is of particular importance for species recovering from past human exploitation, such as the *A. gazella* and *A. tropicalis* populations at Macquarie Island. The number of *A. gazella* and *A. tropicalis* at Macquarie Island, and other Southern Ocean breeding sites, are low due to slow recovery rates following sealing in the 18th and 19th century (SCAR-EGS, 2008; Goldsworthy *et al.*, 2009). As there is an increased likelihood of extinction due to stochastic processes when populations are small (Boyce, 1992; Trillmich, 1993), knowledge of the survival rates of these species in response to climate and oceanographic changes at annual and lifetime scales is necessary to develop a population viability analysis for the Macquarie Island species.

Life Histories of *A. gazella* and *A. tropicalis*

Many models incorporating demographic responses of species to environmental variation assume the main determinant of a species' survival response is their ecological niche and habitat availability (Siniff *et al.*, 2008). Therefore, the sympatric *A. gazella* and *A. tropicalis* at Macquarie Island, which breed within the same bays and occupy the same ecological niche, would be expected to have similar demographic responses to environmental variability (Goldsworthy *et al.*, 1997b; Robinson *et al.*, 2002). However, the response of sympatric populations to environmental conditions differ between species. While the mechanism influencing asynchronous demographic responses has been linked to changes in prey and predator abundance, differences in a specie's life history is another important factor (Forcada *et al.*, 2006; Younger *et al.*, 2016). Therefore, the survival responses of *A. gazella* and *A. tropicalis* to environmental variation may differ due to their differing life histories (Table 1).

As congeneric members of the Otariidae family, *A. gazella* and *A. tropicalis* are similar in many aspects of their life histories (Wickens and York, 1997). Adult fur seals are characterised by sexual bi-maturism as well as pronounced male-biased sexual dimorphism (Table 1) (Payne, 1978). Female fur seals reach sexual maturity at three to four years. Males reach sexual maturity a year or two after females but do not become socially mature and start breeding until approximately eight years old (Laws, 1977; Dabin *et al.*, 2004). The timing of sexual maturity for both sexes can vary among colonies and usually occurs at a younger age in recovering populations (Sutherland *et al.*, 1986). When males become sexually mature they have a 'resource defence polygyny' mating system. Adult males arrive at the breeding beaches between October and November, two weeks before the females (Arnould and Duck, 1997). Single males establish and defend territories where harems of five to 15 females gather. Unless beaten by a challenger and evicted from the breeding beaches, males will fast for two months to defend territories (Arnould and Duck, 1997; Goldsworthy *et al.*, 1999; Lancaster *et al.*, 2007b). Males that are too young, old or incapable of establishing or holding a breeding territory gather at non-breeding beaches referred to as 'bachelor parks' (Kirkwood and Goldsworthy, 2013). Peak mating for each species occurs at different months throughout the season (Wickens and York, 1997) (Table 1). Gestation including a four-month period of delayed implantation, lasts 11.75 months (Riedman, 1990). All females have delayed implantation, allowing the seals to give birth

around the same time each year during the highly productive austral summer months, with ovulation occurring six to nine days after birth.

Females give birth to a single pup, and five to ten days post-partum begin to alternate between time ashore suckling their pup and short foraging trips to replenish milk and energy reserves (Gentry and Kooyman, 1986; Staniland and Robinson, 2008; de Bruyn *et al.*, 2009). While provisioning their pups, *A. gazella* and *A. tropicalis* females at Macquarie Island have similar foraging behaviours and diet (Goldsworthy *et al.*, 1997b; Robinson *et al.*, 2002). Both species forage 30 to 60 km North of Macquarie Island along the Macquarie Ridge, concentrating their foraging efforts at the Macquarie Ridge gap (Robinson *et al.*, 2002). The Antarctic Circumpolar Current passes through the Macquarie Ridge gap creating eddies and an area of high productivity, which supports a large biomass of Myctophidea, in particular *Electrona* spp. the main prey species (93 %) of the *A. gazella* and *A. tropicalis* (Goldsworthy *et al.*, 1997b; Robinson *et al.*, 2002; Flynn and Williams, 2012; Rintoul *et al.*, 2014). However, there is little information available on the foraging behaviour of the sympatric fur seal species during the non-breeding season. The implication of this in terms of modelling demographics is, that there is a limited ability to model and predict demographic responses to environmental or ecological changes during the winter season.

The milk of both species is high in fat and protein enabling the pups to grow and gain mass quickly, however the lactation strategies for each species differ significantly, resulting in differences in the weaning age of the pups (Table 1) (Goldsworthy, 1992). *Arctocephalus gazella* evolved in the highly seasonal environment south of the Antarctic Polar Front (APF) and as a consequence have a brief lactation period (three to four months) to exploit the increased food abundance in the summer. *A. tropicalis* evolved in the less seasonal, temperate waters north of the APF (Repenning, 1975; Gentry and Kooyman, 1986). The waters north of the APF are characterised by low but stable resource availability, requiring *A. tropicalis* to have longer lactation periods of nine to 11 months. *Arctocephalus gazella* gain between 76 and 90 grams per day (Doidge *et al.*, 1984) and wean abruptly at around three to four months, leaving the breeding grounds to forage independently (Riedman, 1990; Wickens and York, 1997). In contrast, *A. tropicalis* gain around 45 grams per day, are weaned gradually and start to display independent foraging behaviour between five and six months (Baylis *et al.*, 2005), with lactation lasting nine to 11 months. Although the life histories of *A. gazella* and *A.*

tropicalis are similar in many respects (Table 1), the differing lactation periods (three to four months vs. nine to 11 months, respectively) and consequential resource provisioning may lead to varying pup survival rates between the species during periods of low prey availability (Goldsworthy *et al.*, 1999).

The Study Site - Macquarie Island

Location

Macquarie Island (54° 30' S, 158° 57' E), lies approximately halfway between Australia and Antarctica, and in 1997 became a World Heritage area. Macquarie Island lies atop of the Macquarie Ridge; formed by the convergent boundaries where the Australian plate meets the Pacific plate. North of the Antarctic Polar Front, the Macquarie Ridge forms one of the main obstructions to the Antarctic Circumpolar Current, generating a high degree of turbulence and current variability in the east (*i.e.* downstream) of the ridge (Rintoul *et al.*, 2014). The island is approximately 34 km long and five km wide with an area of 128 km^2, and is composed of ocean crust, first emerging from the sea 700,000 years ago (Williamson, 1988). Below the steep rising cliffs, the coastal areas provide suitable breeding habitats for pelagic birds, penguins and seals. The main breeding beaches of the recovering fur seal population on the island are at North Head (Figure 3). *Arctocephalus gazella* favour the pebbled beaches of Aerial Cove and Secluded Beach. *Arctocephalus tropicalis* can be found at the southern end of Secluded Beach where the substrate transitions from pebbles to boulders, as well as the boulder coastal areas of Goat Bay and Garden Cove (Lancaster *et al.*, 2010).

Table 1. Summary of life histories of the *Arctocephalus gazella*, *Arctocephalus tropicalis* and *Arctocephalus forsteri*. Adapted from (Riedman, 1990).

	Time of ovulation (days)	Delayed implantation (months)	Duration of lactation (months)	Pup season	Peak mating
A. gazella	6 - 7 after birth	4.2	3.7 - 4	Nov. - Dec.	Mid. Dec.
A. tropicalis	8 - 12 after birth	4.3	9 - 11	Nov. - Dec.	Late Dec. - Jan.
A. forsteri	8 - 9 after birth	4.2	10 - 12	Mid. Nov .- mid. Jan.	Late Dec. - early Jan.

	Adult Male weight (kg)	Adult Female weight (kg)	Male Pup weight at birth (kg)	Female pup weight at birth (kg)	Male sexual maturity (years)	Female sexual maturity (years)	Migration pattern
A. gazella	190	45	5.2	5.9	3 - 4	3 - 4	Seasonal migration
A. tropicalis	88 - 165	35	4.4	4.0	3 - 4	4 - 6	Seasonal movements
A. forsteri	180 - 200	39	3.9	3.3	5 - 6	2 - 5	Non-migratory

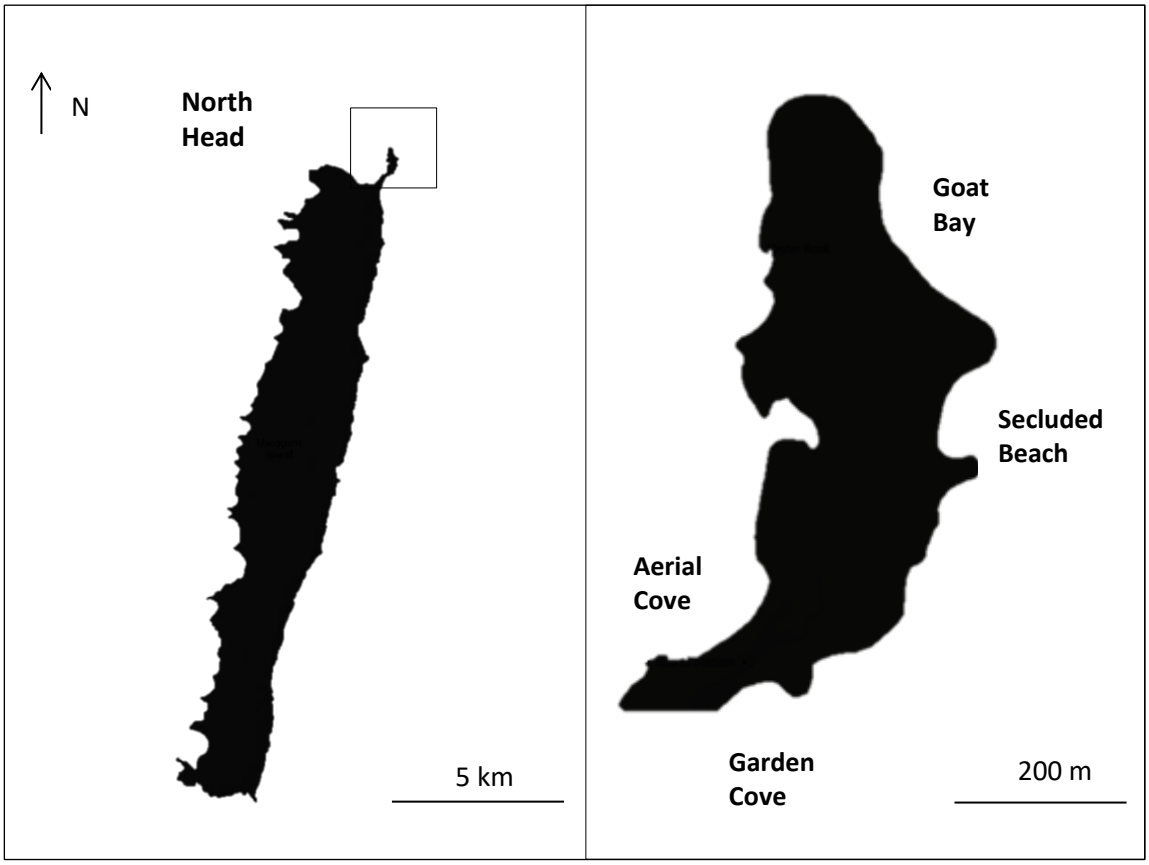


Figure 3. Macquarie Island (54° 30' S, 158° 57' E), illustrating the primary *Arctocephalus gazella* and *Arctocephalus tropicalis* breeding sites (enlarged inset on right).

History of the fur seals at Macquarie Island

The *A. gazella* and *A. tropicalis* breeding populations at Macquarie Island are some of the most distant populations from their major breeding population centres (South Georgia and Gough Island, respectively) (Wynen *et al.*, 2000). The unique occurrence of three species of fur seals on the same island is likely due to this fact combined with the consequences of sealing in the 18th and 19th century.

Commercial sealing began in the Southern Ocean in the 18th century; 102 vessels were operating in the Southern Ocean by 1791; each vessel carrying on average 200 tonnes of

fur and oil per trip (Pearson, 1983). As one of the most southern islands, Macquarie Island was not discovered until 1810 by Frederick Hassleburgh who noted the island was teeming with seals (Poland, 1892; Cumpston, 1968; Kerr, 1976). Named the "Upland seal" by French naturalist René-Primevere Lesson, the exact pre-sealing species on the island is unknown (Hamilton, 1843 in Richards, 1994). Lesson's description of the seal as being small and exclusively inhabiting Macquarie Island and the Penantipodes suggests the species may have been *A. tropicalis*, *A. forsteri*, or a now extinct species (Shaughnessy and Fletcher, 1987b; Taylor, 1990). A recent study which utilised accident DNA technology found no comparison between "Upland seal" DNA and *A. forsteri* or *A. tropicalis* DNA, suggesting that the "Upland Seal" may have been a now extinct species (Salis *et al.*, 2016).

Within 19-years of the first sealers landing at Macquarie Island the "Upland seal" was locally extinct, with shipping records indicating at least 200,000 skins were taken over that time. The decimation was not restricted to fur seals; as the number of "Upland seals" diminished the Southern elephant seal (*Mirounga leonina*) population at Macquarie Island were increasingly rendered down for their oil, as were the penguin species, Royal penguin (*Eudyptes schlegeli*) and King penguin (*Aptenodytes patagonicus*). The continued human inhabitation of Macquarie Island for the exploitation of *M. leonina* and penguins probably prevented the return of fur seals for over 100 years (Goldsworthy *et al.*, 2009).

In 1919 all sealing licences were cancelled and in 1933 Macquarie Island was declared a sanctuary (Csordas, 1963; Cumpston, 1968). The Australian National Antarctic Research Expeditions (ANARE) set up an over-wintering base on Macquarie Island in 1948 and observed 200 juvenile *A. forsteri* at North Head. By 1955 there were over 500 male adult *A. forsteri* present. The first evidence of breeding came in 1955 when a single pup was sighted with an *A. gazella* mother; female *A. tropicalis* were virtually absent at this time (Csordas, 1963). Female *A. gazella* numbers continued to grow in number after 1955. Male *A. gazella* were not observed until the early 1990s (Goldsworthy, unpublished data). Male *A. tropicalis* also began colonising Macquarie Island during the 1950s, while females did not immigrate until the 1980s (Csordas and Ingham, 1965; Goldsworthy *et al.*, 2009). Despite intersexual and interspecies differences in immigration, pup production steadily increased from 1955, resulting in a high percentage of pups being hybrids (17-30% of the total population) (Lancaster *et al.*, 2006). Due to Macquarie Island's geographical isolation, the recovery of the Macquarie Island fur seal population has been slow. The population

recovery has been monitored consistently from 1986-2011 providing one of the longest-running pinniped monitoring studies.

Factors hindering accurate assessment of survival rates

To efficiently quantify Macquarie Island's fur seal population survival relationship to environmental variability, it is necessary to account for both intrinsic (*i.e.* related to animal biology, life history and behaviour) and extrinsic (*i.e.* non-inherited traits) factors, to eliminate major sources of survival rate bias (Lebreton *et al.*, 1992).

Marker loss

Similar to many pinniped demographic studies, the Macquarie Island population was studied using mark-recapture methods, using plastic flipper tags as the form of identification. As with many external artificial markers, flipper tags are not a permanent form of marking as they can be lost or become unreadable. Quantifying the rate at which external markers are lost is needed to accurately assesses population survival rates, as failure to do so would result in underestimating survival rates by as much as 32.5% (McMahon and White, 2009; Oosthuizen *et al.*, 2010; Schwarz *et al.*, 2012; Meyer *et al.*, 2015), which would invalidate any population survival estimate approach which did not incorporate tag loss estimates.

To accurately model marker loss, animals must be marked with a secondary long-term or permaneat form of identification. Since the mid-1980s internal Radio Frequency Identification Transponder (RFID) tags have been a used as a long-term identification marker in a broad range of species including marine mammals and reptiles, such as seals and turtles (Gibbons and Andrews, 2004, Walker *et al.*, 2012). With a low rate of loss, RFID tags act as a "lifetime barcode" for individual animals (Smyth and Neble, 2013), allowing flipper tag loss to be monitored.

Hybridisation

A factor unique to Macquarie Island is the high rates of hybridisation of the fur seal species with 17–30% of all pups being identified as hybrids; (Lancaster *et al.*, 2007a). As

A. gazella, *A. tropicalis* and *A. forsteri* belong to the same genus, hybridisation between the three species would not normally be expected to affect offspring survival rates. However, in this case the differing lactation periods of the two female species at Macquarie Island may result in survival rate differences between different types of hybrid pups. For example, if lactation length is determined by the mother, and pup growth and development are genetically inherited from both parents, then hybrid pups with an *A. gazella* mother and *A. tropicalis* or *A. forsteri* father may have a lower survival rate due to a reduced weaning period (Goldsworthy *et al.*, 1999). Therefore, an assessment of the potential implications of hybridisation on survival rates is an important first step, before modelling the demographic responses of the sympatric populations to environmental variables.

Study Objectives

The objective of this study was therefore to analyse 26-years of demographic data on individual survival in conjunction with tag loss, genotype, and oceanographic data to provide an assessment of the potential effects of environmental variation on the recovery of the *A. tropicalis* and *A. gazella* populations at Macquarie Island.

Specifically, this thesis aimed to evaluate the individual survival rates of two sympatric fur seal populations relative to environmental variability and to describe those life history traits, which are important for persistence in animal populations by:

1. Using a Bayesian framework to quantify flipper tag loss rates, and differences in the tag loss rates by species, sex and age, and obtain posterior distributions of tag loss probabilities that can then be used as priors in demographic modelling.
2. Using genotypes from mitochondrial DNA and microsatellite analyses, to distinguish pure species from hybrids, to examine how an increase in genetic heterogeneity affects the survival of hybrids in comparison to pure *A. gazella* and *A. tropicalis*.
3. Relating how environmental factors known to affect the demographics of Southern Ocean predators (*i.e.* sea level air pressure, sea surface temperature, and wind speed), affect *A. gazella* and *A. tropicalis* survival rates.

Chapter Two

MODELLING TAG LOSS OF TWO SPECIES OF FUR SEAL AT MACQUARIE ISLAND

D. E. Baird-Bower[1], M. A. Hindell[1], S. D. Goldsworthy[2], C. R. McMahon[1, 3], and L. K. Schwarz[4]

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart Tasmania 7001 Australia
[2] South Australian Research and Development Institute (SARDI), Aquatic Science Centre, 2 Hamra Avenue, West Beach, Adelaide, SA 5024 Australia
[3] Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman NSW, 2088 Australia
[4] Institute of Marine Sciences, University of California Santa Cruz, Long Marine Lab, 115 McAllister Way, Santa Cruz, California 95060 USA

Abstract

Understanding the demography of wild populations relies on the long-term identification of individuals either from unique natural or artificial markings. When marks are lost or loss rate is underestimated, survival rates are underestimated and *vice-versa*. Using implanted Radio Frequency Identification Transponder (RFID) tags as a form of long-term identification, tag loss rates of plastic external flipper tags were estimated for the sympatric Antarctic fur seal (*Arctocephalus gazella*) and subantarctic fur seal (*Arctocephalus tropicalis*) at Macquarie Island over a 17-year period, using a Bayesian multi-event, multi-state method. Tag loss was age-dependant, with *A. gazella* and *A. tropicalis* pups having higher probabilities of losing both tags than juveniles and adults ($\psi_{2:0}$ 27-48%, 3-8% and 3-6% respectively). There was little evidence for differences in the tag loss rates between the sexes and species. Under the general assumption that multiple tags on the same individual are lost independently led to an underestimate of survival rates by as much as 16.2%. The tag loss estimates from this study allow us to quantify how survival is affecting population growth rates in this unique population that is recovering from local extinction and shows that the recovering population is growing at a substantially lower rate than other similar colonies. Furthermore, the dependant tag loss estimates presented here could be applied to other studies where permanent marking was not undertaken.

Keywords: Bayesian, mark-recapture, vital rates, *Arctocephalus gazella, A. tropicalis*

Introduction

Quantifying vital rates such as survival and fecundity are fundamental to understanding population dynamics over time. However, collecting these data is not always straightforward, especially for long-lived animals, because it generally requires individual animals to be followed throughout their lives. To do this, animals need to be uniquely identifiable with long-lived and recognisable marks. These marks can take many forms and include natural markings such as skin or fur patterns, or genetic markers (Caudron *et al.*, 1998; Arzoumanian *et al.*, 2005; Karanth *et al.*, 2006; Schwartz *et al.*, 2007; Fernandez-Juricic *et al.*, 2009). While reliable, these identifiers typically require intensive post-observation processing to assign individual identity. Alternatively, animals can be marked with external artificial markers that are unique and easily recognisable. These include single or multiple plastic tags attached to ears or flippers, metal bands around birds legs, collars around necks and brand or tattoo marks (Diefenbach and Alt, 1998; Gauthier-Clerc *et al.*, 2004; McMahon *et al.*, 2006a; McMahon *et al.*, 2006b; McMahon *et al.*, 2007; McMahon and White, 2009). Despite the ease with which animals can be recognised using external markers, they have several limitations. Many are not permanent with tags becoming lost and/or unreadable. Consequently, rates of mark-loss need to be quantified, and included in the subsequent analyses to accurately estimate survival (Bradshaw *et al.*, 2000; McMahon and White, 2009; Oosthuizen *et al.*, 2010).

To estimate tag loss rates, a number of errors need to be quantified, and these fall into two broad categories, extrinsic factors *i.e.* statistical errors and intrinsic factors *i.e.* factors related to animal biology, life history and behaviour. The latter may also include environmental factors including: mark bleaching, biofouling and terrain structure (Bradshaw *et al.*, 2000; Chilvers and MacKenzie, 2010; Dicken *et al.*, 2011). Environmental factors are not uniform over time, therefore, to account for intrinsic loss rates, long-term monitoring of those factors related to tag loss is crucial. Quantifying statistical error is more challenging. Unless an animal is permanently marked independently, the rate of a non-permanent multiple mark loss cannot be observed. Many studies have calculated the probability of an animal losing both tags by squaring the observed probability of an animal losing a single tag; *i.e.* there is an inherent assumption that the probability of losing a second tag is equal to the probability of losing the first tag (x) and hence the probability of losing both tags is x^2 (Seber and Felton, 1981; Wilkinson and Bester, 1997; Bradshaw *et al.*, 2000). However, an increasing number of studies have found that the probability of

losing both tags was greater than under the assumption of independence (McMahon and White, 2009; Schwarz *et al.*, 2012). Indeed, under the assumption of independence, survival rates can be underestimated by as much as 32.5% (McMahon and White, 2009).

The recovering population of sympatric fur seals at Macquarie Island has had a complex re-colonisation history and is experiencing a slow recovery following local extinction (Goldsworthy *et al.*, 2009). Since re-colonisation in the 1950s, Macquarie Island has become a habitat for three species of fur seals: Antarctic (*Arctocephalus gazella*), subantarctic (*Arctocephalus tropicalis*), and New Zealand fur seals (*Arctocephalus forsteri*), all three of which have hybridised (Lancaster *et al.*, 2006; Goldsworthy *et al.*, 2009). Between 1986 and 2011, a long-term capture-mark-recapture study was undertaken. Since 1994, fur seals were tagged with both plastic flipper tags and an implanted Radio Frequency Identification Transponder (RFID) tag. The implantation of an RFID tag acted as a long-term identification marker to identify individual seals if both flipper tags were lost. RFID tags have a low likelihood of failing, allowing individual seals to be identified throughout their lifetime. The loss/failure rate of RFID tags is between 0.004% and 12.1% (Feldheim and Gruber, 2002; Lord *et al.*, 2008), with many reports citing a retention rate of 95% to 100% (Galimberti *et al.* 2000; Gibbons and Andrews, 2004; Beausoleil *et al.* 2004; Smyth and Nebel, 2013). As such, the implantation of an RFID tag provided a means to identify seals in the event that both flipper tags were lost.

Using 17-years (1994–2011) of individual capture-mark-recapture observations where RFID tags were used, we developed a Bayesian analysis to estimate flipper tag loss rates for *A. gazella* and *A. tropicalis* at Macquarie Island. Specifically, we aimed to: (i) quantify age-, sex- and species-specific tag loss rates (ii) determine differences in survival rate estimate when tag loss is and is not accounted for and (iii) obtain tag loss probabilities that can be used in future analyses evaluating the demography of the sympatric fur seal population at Macquarie Island and other populations.

Methods

Historical information

Commercial sealing in the Southern Ocean during the 18th and 19th century led to the extinction of the fur seal population at Macquarie Island (Shaughnessy and Fletcher, 1987a). The first indications of re-colonisation were not documented until 1948 when 200 juvenile *A. forsteri* were observed at the Island (Csordas, 1963). However, it was not until after the 1980s that the population began to grow more rapidly albeit at rates lower (8.6% for *A. gazella* and 6.8% *A. tropicalis;* Goldsworthy *et al.*, 2009) than other recovering fur seal populations (*e.g.* 17.1% at Marion Island and 9.3% – 12.7% at Prince Edwards Island) (Bester *et al.*, 2003; Hofmeyr *et al.*, 2006b; Goldsworthy *et al.*, 2009). The key reasons for these slow recovery rates have been attributed to Macquaire Islands isolation from the major population centres, intersexual differences in the timing of colonisation, and extensive hybridisation among species (Goldsworthy *et al.*, 2009). To better understand the factors contributing to the slow and complex re-colonisation at Macquarie Island, a capture-mark-recapture study was initiated in 1986 to provide detailed demographic data on the population.

Tagging

Fieldwork was undertaken on the North Head Peninsula, Macquarie Island (54°30'S, 158 °56'E) between 1986 and 2011. Over this period, annual pup production of all species (including hybrids) in the population increased from 37 to 260, with most pups flipper tagged as part of an annual monitoring program. A total of 3606 pups and 713 adult fur seals were tagged over this time (Table 1). The breeding population of fur seals on Macquarie Island consists of *A. gazella* and *A. tropicalis*; and although male *A. forsteri* are numerous (especially during the summer), and on occasion breeding with female *A. gazella* and *A. tropicalis*. There are no breeding females (Goldsworthy *et al.*, 2009), therefore *A. forsteri* were removed from this analysis.

Arctocephalus gazella, *A. tropicalis, A. forsteri,* and hybrid pups were captured one to three weeks after birth and temporarily marked by bleaching their fur and their species or hybrid status was determined based on an integrated phenotype score of pelage colouration and pattern (Shaughnessy *et al.*, 1988a; Goldsworthy *et al.*, 1997a). This was reliable for pure

species, with *A. gazella* and *A. tropicalis* pups being correctly identified in 96.6% and 92.4% of cases, respectively (Goldsworthy *et al.*, 2009). However, only 25.3% of hybrid pups were correctly identified, with 74.7% being misidentified as pure species. Pups were captured for a second time, usually a month after birth when beginning to moult, and tagged with a Dalton Superflexitag® (embossed on the tag's outer surface with four to five unique numeric characters) inserted in the trailing edge of each fore-flipper. Pups which died prior to being tagged were recorded as dead and never tagged. All taggers were trained by an experienced field worker to ensure that tagging was standardised throughout each breeding season. Pups were also weighed, and sexed. From 1994 onwards, all tagged pups were also marked with a RFID tag. The highest rate of RFID tag loss occurs shortly after implantation (before the wound is healed) most likely due to the body recognising the tag as a foreign object and expelling it (Gibbons and Andrews, 2004). Prior to the insertion of the RFID tag, the implantation site was cleaned with an antiseptic solution to reduce the chance of infection, and likelihood of tag loss. The RFID tag was inserted subcutaneously on the dorsal mid-line between the pelvis and base of the tail. All RFID tags were tested after insertion to ensure readability by the receiver. While the RFID tag provides a long-term means of identification they require close contact with the seal to be read. Alternatively, flipper tags provide a simple and non-invasive method to easily resight individual seals from a distance, albeit the marking is not always permanent throughout an animal's lifetime.

Resights and retagging

Resighting of marked seals was undertaken approximately daily between November and March from 1986/87 to 2011/12, excluding 2004/05. Resights were conducted from the edge of the breeding territories using binoculars, as the tags can be read from a distance of ten meters, minimising disturbance to the seals. At the end of the breeding season, observers could enter the breeding territories, because the adult seals had left the breeding aggregations, and seals missing one or both tags (identified by the presence of tag hole/ rip in the fore-flipper) were opportunistically scanned for an RFID tag, captured and retagged. New flipper tags were only attached to flippers which did not contain a flipper tag; and when possible, new flipper tags were inserted in the hole left by an earlier tag, to avoid the creation of additional scar tissue. Furthermore, if a seal did not have an RFID tag (tagged before 1994, not microchipped at the time of tagging, or RFID tag failed), a

new RFID tag was inserted. Long-term identification of individual seals, which were retagged, was managed by matching and recording a seal's new flipper tag ID to their original flipper tag ID and/or their RFID number.

Analysis

Dependant tag loss probabilities (*i.e.* the loss of a second tag being dependant on the loss of the first tag), were estimated with a Bayesian multi-event, multi-state model, using seals tagged with multiple flipper tags and an RFID tag. A total of four parameters defined an individual's transition from one state to another at each resighting event: survival probability (Φ), resight-probability (p), probability of losing tag(s) (ψ), and probability of detecting a RFID tag ($\boldsymbol{d}_R$) (Table 2; Appendix A). Retagging was incorporated into the model through the addition of five states, which can be matched to the Markovian matrix (Appendix A).

1. Alive, one tag counted then retagged to have two tags, no RFID tag

2. Alive, one tag counted then retagged to have two tags, RFID tag detected

3. Alive, one tag counted then retagged to have two tags, RFID tag not detected

4. Alive, zero tag counted then retagged to have two tags, RFID detected

5. Alive, zero tag counted then retagged to have one tag, RFID detected

Within an annual time step an animal which was retagged would move from one state to another. For example, an animal seen at time t with one tag, which was then retagged with an additional tag was recorded as a different state. Then at $t+1$ the animal would be recorded as having had two tags and the probability of transitioning from a tagging state would be recorded as $\psi_{2:x}$.

Preliminary analysis found that tag loss rates as a function of age had wide credible intervals, reflecting the relatively small sample size in each annual age class (Appendix B). Therefore, tag loss was estimated for just three age classes: pups, juveniles and adults. Pups were animals less than one year old. *Arctocephalus gazella* and *A. tropicalis* have different ages of sexual maturity, so juvenile *A. gazella* were aged one and three, while juvenile *A. tropicalis* were one to four years of age (Payne, 1977; Bester, 1987). Adult *A.*

gazella were those aged four years and older, and *A. tropicalis* were aged five years and older. The main breeding aggregations of the *A. gazella* are on pebble beaches, while *A. tropicalis* inhabit boulder coves (Lancaster *et al.*, 2010). As Bradshaw *et al.* (2000) demonstrated, *A. forsteri* are more likely to lose tags where the terrain was comprised of small rocks and crevices compared to pebbled beaches. Given the fine-scale species substrate segregation of the Macquarie Island population, tag loss rates were also estimated for each species. It was hypothesised *A. tropicalis* which breed on boulder beaches would have a higher tag loss rate than *A. gazella* which breed on pebble beaches, as tags are less likely to snag on pebbles. In addition, *A. gazella* and *A. tropicalis* are a sexually dimorphic species, with different intra-specific growth rates and behaviours, which can affect tag loss (Wickens and York, 1997; Guinet *et al.*, 1999; McMahon and White, 2009; Schwarz *et al.*, 2012). Therefore, tag loss was also estimated for each sex. Lastly, the uncertainty in the probability of an animal moving from a tagged state to a zero-tag state ($\psi_{2:0}$, $\psi_{1:0}$) was dependant on RFID tag detection effort, which was measured by the number of times the RFID tag was checked. RFID tag detection was estimated annually by incorporating two different states, *i.e.* scanned or not scanned into the model, dependent on whether an animal was scanned for an RFID tag or not.

Table 1. The number of fur seal pups tagged, subset by species and sex. Pups whose sex and/or species could not be identified are labelled unknown (*N* = 3606).

Year	***Arctocephalus tropicalis***		***Arctocephalus gazella***		***Arctocephalus forsteri***		**Hybrid**		**Unknown**
	n = 698		*n* = 2270		*n* = 157		*n* = 325		*n* = 156
	Male	Female	Male	Female	Male	Female	Male	Female	
1986	1	6	7	14	6	-	-	-	6
1887	5	4	11	8	4	-	-	-	4
1888	5	6	10	14	9	-	-	-	9
1989	7	6	7	9	19	1	6	5	19
1990	8	7	18	18	-	-	6	2	-
1991	10	12	22	17	-	-	12	4	-
1992	8	11	39	19	1	-	4	1	1
1993	11	9	33	36	-	-	3	1	-
1994	6	11	42	35	1	-	7	1	1
1995	16	7	43	38	2	-	6	3	2
1996	6	15	50	42	11	-	5	2	11
1997	12	16	54	42	-	-	8	4	-
1998	16	12	40	44	5	-	9	10	5
1999	6	4	34	38	53	-	12	5	53
2000	12	18	45	68	3	-	5	2	3
2001	14	17	64	46	5	-	4	2	5
2002	25	16	30	40	1	-	20	19	1
2003	15	19	50	61	8	-	4	2	8
2004	9	5	29	29	1	-	1	-	1
2005	12	20	66	70	12	-	11	3	12
2006	23	14	80	70	14	-	4	3	14
2007	21	21	86	62	-	-	8	5	-
2008	26	22	68	70	-	-	13	7	-
2009	27	21	59	66	1	-	30	19	1
2010	28	22	53	90	-	-	24	13	-
2011	21	27	89	95	-	-	8	2	-

Table 2. Description of all states for each transition parameter within the Bayesian multi-state multi-event model.

Transition parameters	States
Survival probability	Alive, Dead
Resight-probability	Seen, Not seen
Probability of losing tags*	$\psi_{2:2}$, $\psi_{2:1}$, $\psi_{2:0}$, $\psi_{1:1}$, $\psi_{1:0}$
Probability of detecting RFID tag	Detected, Not detected

* ψx:y is the probability of transitioning from x-tag state to y-tag state *e.g.* ψ2:0 is the probability of going from two tags to no tags within a year.

The Bayesian multi-event, multi-state models were based on the standard Cormack-Jolly Seber (CJS) mark-recapture model (Lebreton *et al.* 2009), and created in the Fortran program MTG (Metropolis within Gibbs: a Markov chain semi-random walk simulation procedure) developed by Daniel Goodman (Schwarz, 2008). Parameters were given uniform priors between zero and one. Simulations were set for a rejection rate near 0.7, a sub-sampling (thinning) of one in 50 and a burn-period of 50 for each inference. The resulting lag-1 auto-correlations were <0.1, and independent chains with different parameter starting values gave indistinguishable results. Log ratios were used to calculate differences between cohort groupings. To verify convergence and stationarity within the final chains, we used the Heidelberger and Welch convergence diagnostic available from the CODA package in R using standard 10% increments and $p \leq 0.05$ (Heidelberger and Welch, 1983; Plummer *et al.*, 2006).

Results

Effects of age, sex and species on tag loss

Tag loss varied with age so that the probability of losing both tags ($\psi_{2:0}$) was higher for pups than both other age classes (Figure 1). The mean probability of a pup losing both tags was 0.48 with a 95% credible interval (CI) of 0.41, 0.54 for female *A. gazella* and 0.27 (95% CI 0.21, 0.35) for males. This is in contrast to the mean probability of 0.06 (0.05, 0.08) for adult female *A. gazella* and 0.02 (0.01, 0.04) for males. Juvenile *A. gazella* and *A.*

tropicalis had similar tag loss probabilities to adults for all tag loss transition probabilities (Figure 1). Our results showed the mean probability of a juvenile *A. tropicalis* transitioning from two tags to one tag was 0.06 (0.008, 0.17) per year for females and 0.07 (0.008, 0.017) for males. This is similar to the mean probability of 0.07 (0.03, 0.10) for adult female *A. tropicalis* and 0.04 (0.01, 0.07) for adult males.

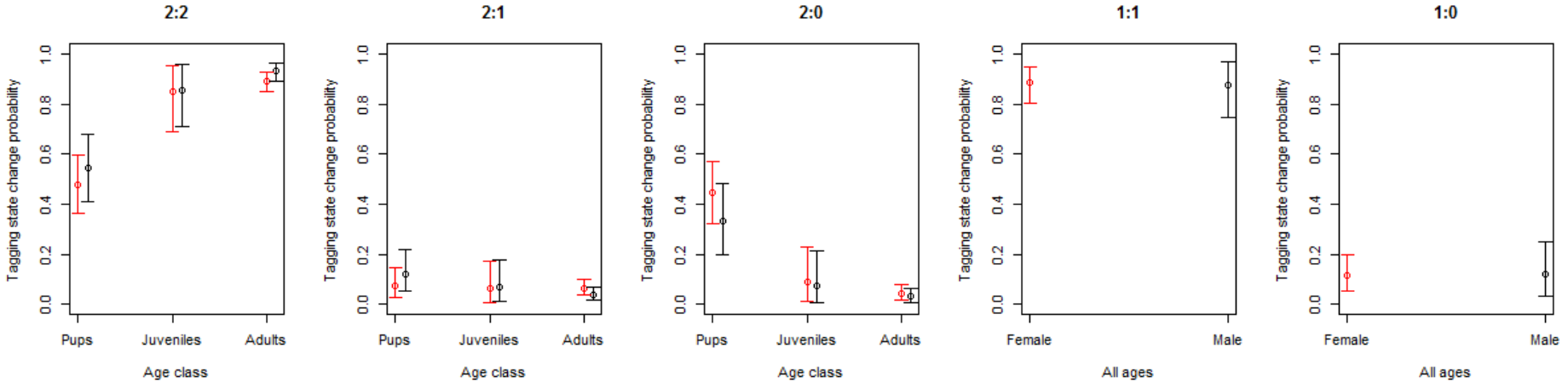
Sex differences in tag loss rates were only found in the pup age class. The probability of a female *A. gazella* pup keeping both tags ($\psi_{2:2}$) was 20.7% lower than their male counterparts. Consequently, female *A. gazella* pups had a greater probability of transitioning from two tags to zero tags ($\psi_{2:0}$) than male *A. gazella* pups. In general, sex had no effect on tag loss probabilities in all other age classes.

Accounting for sex and age class, there was limited evidence of differences in tag loss rates between species (Figure 2), although *A. gazella* had a lower variation in tag loss probability compared to *A. tropicalis* due to a difference in sample size (Figure 1 and Table 1). The one exception was the probability of juveniles transitioning from a two-tag state to a one-tag state. Male juvenile *A. tropicalis* had a greater probability of transitioning from two tags to one tag ($\psi_{2:1}$) than male juvenile *A. gazella* (Log ratio: -1.37 (-3.58, 0.85)).

Most importantly, tag loss rates were dependant *i.e.* first year pups had a greater probability of transitioning from a two-tag state to a zero-tag state ($\psi_{2:0}$) than to a one-tag state ($\psi_{2:1}$). This meant that the observed rates of double tag loss for female *A. gazella* pups were 16.2% greater than the loss rates that would be predicted under the assumption of independence *i.e.* the single loss rate squared. For male *A. gazella* pups dependant tag loss rates were 3.5% lower than independent predictions, and for female and male *A. tropicalis* pups it was +15.6% and -4.9% respectably. Past the age of two years, all cohorts had low two tag and one tag loss probabilities ($\psi_{2:1}$, $\psi_{1:0}$, $\psi_{2:0}$), and a high probability of retaining a single tag ($\psi_{1:1}$) or both tags ($\psi_{2:2}$) (Figure 1).

RFID tag detection probabilities (for seals that had lost both flipper tags) were estimated by year, species, and sex. Resight effort, which was measured by the number of times the RFID tag was checked, varied between years for male and female *A. gazella* until 2008, when RFID tag resight effort increased (Table 3). While *A. tropicalis* RFID tag resight efforts were consistently low from 1994 to 2005 for both sexes, resight efforts increased after 2008 (Table 3).

Arctocephalus tropicalis



Arctocephalus gazella

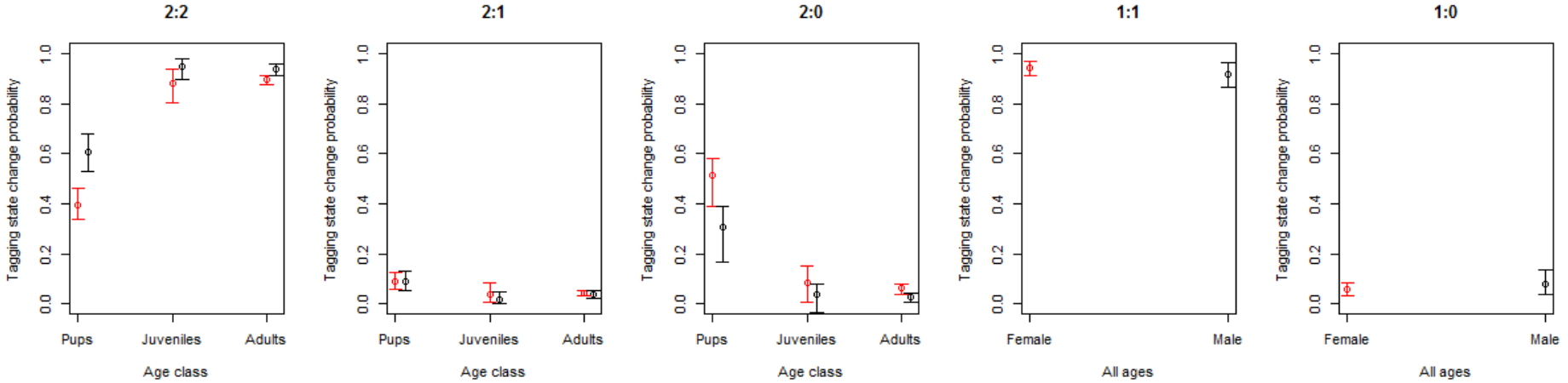


Figure 1. Posterior distribution of tag loss transition probabilities as a function of age classes, sex and species. $\psi_{x:y}$ is the probability of transitioning from the x-tag state to the y-tag state *e.g.* $\psi_{2:0}$ is the probability of going from two tags to no tags within a year. Points are means and bars are 95% posterior intervals. Females are red, and males are black. Sample size for $\psi_{1:1}$ and $\psi_{1:0}$ was limited, so cohorts were grouped as all ages.

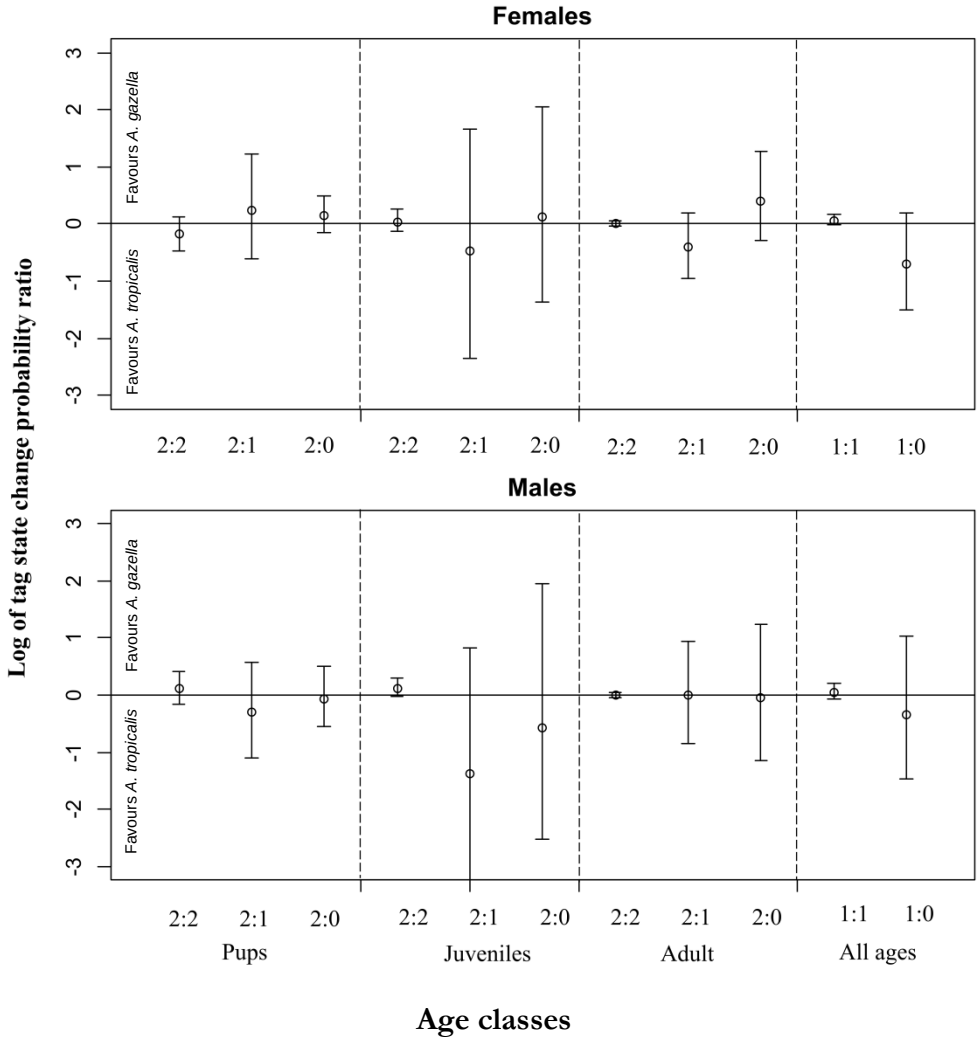


Figure 2. Log probability ratio of the tag state change of *Arctocephalus gazella* and *Arctocephalus tropicalis* grouped by sex and age classes. Values over zero indicate *A. gazella* are more likely to make the transition than *A. tropicalis*. Points are means and bars are 95% posterior intervals.

Unexpectedly, the probability of detecting an animal with one tag was greater than detecting two tags on an animal. Overall, tag status was determined more often in females than males, and in *A. gazella* than *A. tropicalis* (Table 4).

Table 3. Probability of detecting an implanted Radio Frequency Identification Transponder (RFID) tag, which is a function of an animal retaining an RFID tag and the search effort to scan an animal for an RFID tag, by survey year, sex and fur seal species. Marginal means with 95% credible intervals given in parentheses.

	Arctocephalus tropicalis		***Arctocephalus gazella***	
Year	Female	Male	Female	Male
1995	0.39 (0.01, 0.94)	0.44 (0.02, 0.96)	0.37 (0.01, 0.94)	0.36 (0.01,0.94)
1996	0.39 (0.10, 0.74)	0.23 (0.01, 0.71)	0.29 (0.07, 0.61)	0.30 (0.04,0.71)
1997	0.20 (0.03, 0.53)	0.13 (0.00, 0.46)	0.13 (0.02, 0.35)	0.15 (0.00,0.53)
1998	0.06 (0.00, 0.20)	0.10 (0.00, 0.36)	0.09 (0.01, 0.25)	0.41 (0.09,0.85)
1999	0.05 (0.00, 0.18)	0.09 (0.00, 0.31)	0.07 (0.01, 0.19)	0.11 (0.00,0.39)
2000	0.09 (0.01 ,0.23)	0.16 (0.02, 0.41)	0.32 (0.18 ,0.49)	0.29 (0.06,0.64)
2001	0.19 (0.06, 0.36)	0.15 (0.02, 0.40)	0.25 (0.13 ,0.40)	0.17 (0.03,0.39)
2002	0.21 (0.07, 0.41)	0.07 (0.00, 0.25)	0.08 (0.02, 0.18)	0.05 (0.00,0.19)
2003	0.24 (0.09, 0.43)	0.07 (0.00, 0.25)	0.46 (0.33, 0.59)	0.23 (0.08,0.43)
2004	0.04 (0.00, 0.13)	0.08 (0.00, 0.27)	0.02 (0.00, 0.07)	0.04 (0.00,0.16)
2005	0.11 (0.02, 0.25)	0.08 (0.00, 0.27)	0.10 (0.04, 0.19)	0.07 (0.01,0.20)
2006	0.35 (0.18, 0.53)	0.08 (0.00, 0.27)	0.28 (0.19, 0.39)	0.20 (0.08,0.36)
2007	0.10 (0.01, 0.26)	0.14 (0.02, 0.36)	0.03 (0.01, 0.08)	0.03 (0.00,0.11)
2008	0.34 (0.15, 0.57)	0.45 (0.24, 0.68)	0.32 (0.23, 0.42)	0.39 (0.26,0.54)
2009	0.52 (0.28, 0.77)	0.45 (0.23, 0.69)	0.42 (0.31, 0.54)	0.56 (0.39,0.73)
2010	0.13 (0.02 ,0.36)	0.41 (0.16, 0.72)	0.48 (0.33, 0.64)	0.31 (0.14,0.52)
2011	0.60 (0.27, 0.95)	0.57 (0.21, 0.96)	0.34 (0.19, 0.53)	0.47 (0.23,0.78)

Table 4. Probability of assigning tag status by the number of tags and sex for Radio Frequency Identification Transponder (RFID) tagged fur seals. Marginal means with 95% credible intervals given in parentheses.

	Arctocephalus tropicalis		***Arctocephalus gazella***	
Number of tags	Female	Male	Female	Male
1	0.64 (0.53, 0.74)	0.57 (0.42, 0.71)	0.76 (0.71, 0.80)	0.64 (0.56, 0.71)
2	0.51 (0.45, 057)	0.39 (0.32, 0.46)	0.64 (0.61, 0.66)	0.47 (0.43, 0.51)

Implications of tag loss on survival

In general, mean survival rate estimates that included tag loss were equal to or slightly higher than models that did not account for tag loss. However, results from both models had high uncertainty (Figure 3 and Figure 4). As might be expected from the retagging effort, there was little difference between the survival estimates which did and did not incorporate tag loss estimates *i.e.* the 2001 adult male *A. tropicalis* survival estimates that accounted for tag loss was 0.74 with a 95% posterior interval (PI) of 0.52, 0.89. This is similar to the adult *A. tropicalis* survival estimates that did not account for tag loss (0.68 (95% PI 0.42, 0.95)) (Figure 3). In the most extreme case, the 2008 survival estimates of female *A. gazella* pups, showed a 26.3% survival probability difference between tag loss incorporated survival rates (0.57 (0.41, 0.75)) and survival rates which did not incorporate tag loss rates (0.31 (0.19, 0.45)) (Figure 4).

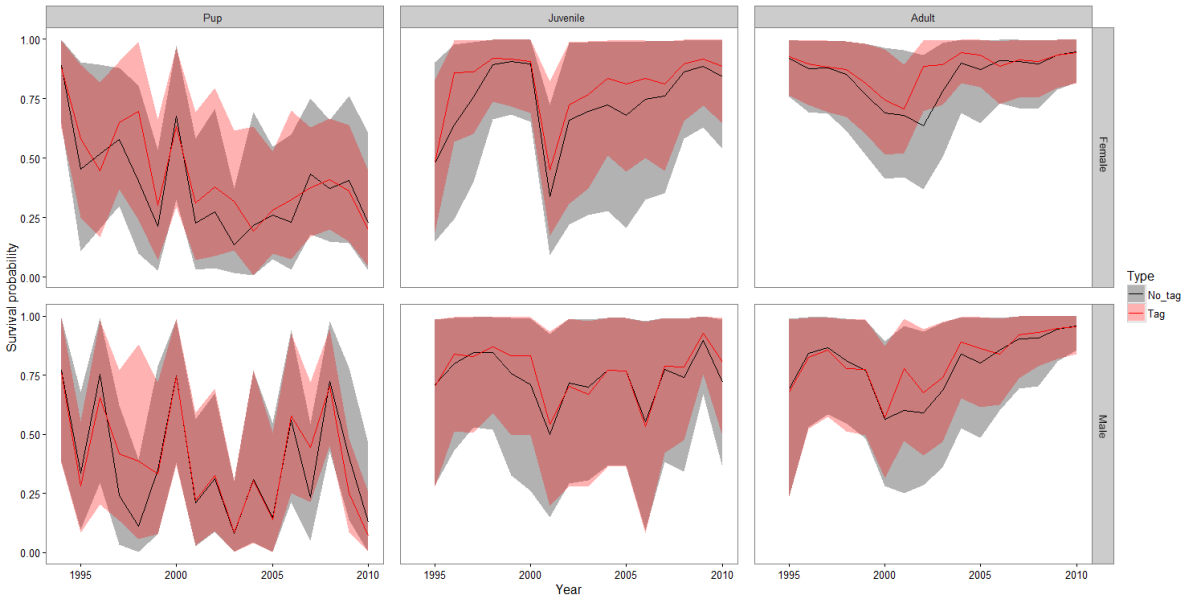


Figure 3. Posterior distributions of annual survivorship estimates of retagged *Arctocephalus tropicalis*, grouped by age class and sex. Survival estimates with tag loss are red, and survival estimates which do not include tag loss are black. Solid lines represent the expected survivorship. Shaded areas are 95% posterior intervals. In general, mean survival rate estimates from models that included tag loss were equal to or slightly higher than models that did not account for tag loss.

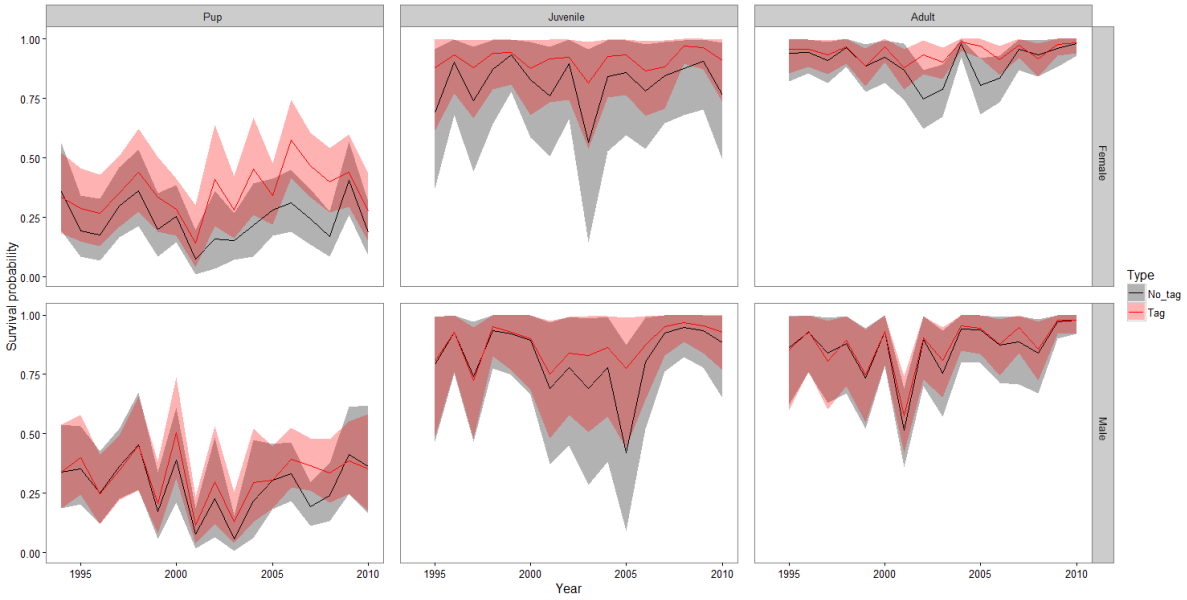


Figure 4. Posterior distributions of annual survivorship estimates of retagged *Arctocephalus gazella*, grouped by age class and sex. Survival estimates with tag loss are red, and survival estimates without tag loss are black. Solid lines represent the estimated mean survival rate. Shaded areas are 95% posterior intervals. In general, mean survival rate estimates from models that included tag loss were equal to or slightly higher than models that did not account for tag loss.

Discussion

Quantifying tag loss is important for understanding population changes over time and providing accurate vital rate estimates. Previous demographic studies of *A. gazella* and *A. tropicalis* used tag loss estimates based on the assumption of independent tag loss rates, as such, these tag loss estimates were probably underestimated (McMahon and White, 2009; Schwarz *et al.*, 2012). Underestimation of tag loss rates, and in turn survival rates, reduces the accuracy in population projections (Rotella and Hines, 2005). This study not only contributes to a broader understanding of tag loss in pinnipeds, but specifically quantified age and sex-specific dependant tag loss estimates for each species of fur seal at Macquarie Island, enabling accurate estimation of survival rates. This will allow exploration of a range of biotic (hybridisation, predation, and/or competition, immigration rates) and abiotic factors (environmental variation) which may be causing the observed population growth rate less than r_{max} (the maximum rate of population increase) (Guinet *et al.*, 1994; Hofmeyr *et al.*, 2005). Results may be particularly important given *A. tropicalis* at Macquarie Island

are listed as threatened due to the low number of mature individuals (Threatened Species Scientific Committee, 2016). This study provides the first dependent tag loss estimate for *A. gazella* and *A. tropicalis* which may be used in other demographic studies of *A. gazella* or *A. tropicalis*.

Tag loss was age-class-specific; with both *A. gazella* and *A. tropicalis* pups having a higher tag loss probability than juveniles and adults. The higher likelihood of tag loss in pups is probably due to their softer flippers, and the tags being more prone to abrasion due to spending more time ashore walking, and pup-specific behaviour, such as time playing and engaging in mock fights while juveniles and adults forage at sea, (Diefenbach and Alt, 1998; Bradshaw *et al.*, 2000). Young mammals also have a less developed immune system than their adult counterparts (Hall *et al.*, 2002), and lower individual immunity may lead to increased risk of infection, and tissue necrosis at the tagging site, as demonstrated in sea turtles (Rivalan *et al.*, 2005). This reiterates the importance of using stage-specific tag loss (pups, juveniles, and adults) in survival models when relaying on non-permanent markings (Oosthuizen *et al.*, 2010; Schwarz *et al.*, 2012).

Sex was found to be a factor in tag loss rates for *A. gazella* pups, with female pups having a higher probability of losing both tags ($\psi_{2:0}$) than males, although the reason for this is unclear. Differences in behaviour or body condition can influence tag loss rates, and this may be the mechanisms behind different tag loss rates for male and female fur seals pups (McMahon and White, 2009). Similar to the Southern elephant seal (*Mirounga leonina*) *A. gazella* and *A. tropicalis* are sexually dimorphic and have differing intra-specific growth rates. As female pups grow more slowly than their male counterparts (Payne, 1978), their smaller body size may increase tag loss rates. Although, it is more plausible males pups engaging in mock fights will increase tag loss rate (Bradshaw *et al.*, 2000). For juveniles and adults, tag loss did not strongly differ by sex or species, unlike other tag loss studies which show that growth rates and behaviours often lead to sex-dependent tag loss rates, in numerous species. (Pistorius *et al.*, 2000; Chilvers and MacKenzie, 2010; Oosthuizen *et al.*, 2010). However, two tag loss studies have also concluded that tag loss rates were independent of sex (McMahon and White, 2009; Schwarz *et al.*, 2012); and we suggest that tag loss rates are independent of sex for adult *A. gazella* and *A. tropicalis* due to the species being of smaller size and life history (Pistorius *et al.*, 2000; Chilvers and MacKenzie, 2010; Oosthuizen *et al.*, 2010). Male *A. gazella* or *A. tropicalis* weigh on average 190 kg and 165 kg respectively, while male New Zealand sea lions (*Phocarctos hookeri*) *and M. leonina* weigh

between 200 kg – 400 kg and 1500 kg – 3500 kg respectively. The heavier weight of male *P. hookeri* and *M. leonina* may cause greater wear and tear on the tags resulting in a higher loss rate. Although, it should be noted, *P. hookeri* tend to occupy sandy beaches, and *M. leonina* are not expected to place much weight on tags (due to their locomotion not involving the rear flippers where tags are placed), reducing the chance of tag wear and tear overall. For males of both species, it is also possible that the thickening of the flipper increases to a dimension larger than that of the tag, causing ulceration around the tag, resulting in tag loss through the subsequent hole. In closing, while tag loss rates did not differ by sex for *A. gazella* and *A. tropicalis* (except in pups) in this study, sex-specific tag loss should still be considered in species that exhibit sexual dimorphism and behavioural traits to avoid sex-specific tag loss bias.

Bradshaw *et al.*, (2000) demonstrated that *A. forsteri* were more likely to lose tags where the terrain was comprised of small rocks and crevices compared to pebbled beaches. *A. gazella* at Macquarie Island inhabit small pebbled beaches while *A. tropicalis* hold territory in bouldered coves (Lancaster *et al.*, 2010), yet there was no difference in tag loss probabilities between species. However, complete spatial segregation (pebbled *vs.* bouldered beaches) of the species is only observed in juveniles and adults. As juveniles and adults have low tag loss rates (2% - 12%), species-specific tag loss rates would be difficult to identify. In addition, pups of both species older than two months move between bays (Lancaster *et al.*, 2010) effectively occupying similar habitats. This apparent dissimilarity between our results and Bradshaw *et al.* (2000) should be interpreted with some caution. In the Bradshaw *et al.*, (2000) study, tagging with swivel tags similar to those used in this study was limited to just 39 individuals over a two-year period (1998–1999).

There are three studies which estimate tag loss rates for *A. gazella* and *A. tropicalis* (Boyd *et al.*, 1995; Beauplet *et al.*, 2005; Schwarz *et al.*, 2013), two of which assumed independent tag loss. The probability of an adult female *A. gazella* losing one tag (0.061 (0.047, 0.077)) was higher than those reported (0.027 (0.021, 0.033)) at Cape Shirreff, (Schwarz *et al.*, 2013), while individual tag loss for *A. tropicalis* at Amsterdam Island (0.217 ± 0.027) (Beauplet *et al.*, 2005) was greater than that observed at Macquarie Island (0.065 (0.008, 0.172)). These differences are attributed to site-specific tag loss, as noted in differing tag loss rates of *M. leonina* between Macquarie Island and Marion Island (Oosthuizen *et al.*, 2010): ascribed to tagging technique, tag placement and physical environment. The dependant tag loss rates of Macquarie Island's *A. gazella* losing both tags ($\psi_{2:0}$) was closer

in value (0.061 (0.047, 0.077)) to those reported for adult females (0.087) at Bird Island South Georgia (Boyd *et al.*, 1995), who assumed independent tag loss. However, in general, calculating independent tag loss estimates creates survivorship bias, which can lead to bias estimates of population size, leading to erroneous management recommendations if independent tag loss bias is not factored into the survival estimates (Rotella and Hines, 2005; McMahon and White, 2009; Schwarz *et al.*, 2012).

Survival bias within our own study should also be noted. RFID tags are not necessarily a permanent method of animal identification. As our tag loss models do not incorporate RFID tag loss, it is subject to biases that underestimates *A. gazella* and *A. tropicalis* survival estimates. Under the assumption *A. gazella* and *A. tropicalis* RFID tag loss mimics the RFID tag loss of *P. hookeri* (Duignan, Wilkinson, and Clark, pers. comm. 2004, as cited in Beausoleil *et al.*, 2004) RFID tag loss can be assumed to occur in 4% to 10% of the RFID tagged fur seal population. This, therefore, creates a survival bias that is 4% to 10% of the probability of *A. gazella* and *A. tropicalis* losing both tags ($\psi_{2:0}$) (Appendix C). Although our survival estimates may be conservative, any bias caused by RFID tag loss/failure does not confound the overall comparison of the effects of age, sex and/or species on survival rates for the Macquarie Island *A. gazella* and *A. tropicalis* population.

The comparable survival rates with and without accounting for tag loss may be attributed to the high retagging effort of this study. Retagging of animals when they have lost one or both tags, such as in Beauplet *et al.*, (2006)'s study, is a useful method albeit a logistically intensive way of ensuring reliable survival probabilities. However, despite, the substantial recapture and retag efforts here it was still not possible to fully negate the need to account for tag loss. It may be argued that the effort of retagging to eliminate tag loss may be too high to be a successful long-term mark-recapture field method, especially in large populations. The high effort of retagging can be seen in the higher probability of detecting an animal with one tag rather than two tags, which is a result of field observers, focusing on retagging animals which have lost both, leading to an increasing number of animals retaining only one tag. Under such conditions, there may be merit in shifting the focus from retagging animals who have lost flipper tags (the number of which will continue to increase as the population grows) to spending more time reading RFID tags to identify individuals who have lost tags.

Given the high variance of tag loss rates due to a range of factors, tag loss rates should where possible be estimated separately for each tagging program to ensure accurate

survival estimates. However, if dependant tag loss rates cannot be estimated, the values presented in this paper can be applied to other studies to overcome survival bias caused by independent tag loss estimates. Incorporating dependant tag loss estimates into pup survival analysis is critically important, given pups high rate of double tag loss.

Acknowledgements

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Ethics

Research was conducted under permit from the Tasmanian Parks and Wildlife Service and conducted with the approval of the Antarctic Animal Ethics (Australian Government, Antarctic Division), the University of Tasmania, and La Trobe PIRSA animal ethics committees.

Chapter Three

THE SLOW ROAD TO RECOVERY: RE-COLONISATION OF TWO SPECIES OF FUR SEAL (*Arctocephalus gazella* and *A. tropicalis*) AT MACQUARIE ISLAND

D. E. Baird-Bower[1], M. A. Hindell[1], C. R. McMahon[1,2], S. D. Goldsworthy[3], M. L. Lancaster[4], and L. K. Schwarz[5]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart Tasmania 7001 Australia
[5]Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman NSW, 2088, Australia
[3]South Australian Research and Development Institute (SARDI), Aquatic Science Centre, 2 Hamra Avenue, West Beach, Adelaide, SA 5024, Australia
[4]Zoos Victoria, PO Box 74, Parkville, Vic. 3052. Australia
[5] Institute of Marine Science, University of California Santa Cruz, Long Marine Lab, 115 McAllister Way, Santa Cruz, California 95060 USA

Abstract

Successful establishment in a new habitat via range expansion or re-colonisation depends on a multitude of biotic and abiotic factors. One of the best examples of successful re-colonisation is the fur seals. Populations of fur seals (*Arctocephalus* spp.) on most sub-Antarctic islands were over-harvested in previous centuries. Although many populations have since experienced rapid population growth, such as the Antarctic fur seal (*Arctocephalus gazella*) population at South Georgia, growing at an annual rate of 14.0%. Other populations, such as those at Macquarie Island, are recovering relatively slowly, with an annual growth rate of 3.4% for subantarctic fur seals (*Arctocephalus tropicalis*) and 8.6% for *A. gazella*. Macquarie Island has three species of fur seals *A. gazella, A. tropicalis* and New Zealand fur seals (*Arctocephalus forsteri*) which all interbreed, representing a unique hybrid zone, with the highest percentage of hybrid pups (17-30% of the total population) of any sympatric seal population. As such, hybridisation has been suggested to be a contributing factor in the slow recovery of the Macquarie Island fur seal populations. To evaluate the potential demographic effects of hybridisation on population recovery rates, we used genetic profiles from mitochondrial DNA and microsatellites to distinguish pure species from hybrids and compared the survival rates of these groups. A Bayesian survival model, based on the standard Cormack-Jolly Seber mark-recapture model, was used to determine whether hybrid individuals had similar survival probabilities to individuals of pure species. Hybrids had similar survival rates to pure species, with hybrid survival rates closer to the survival rates of *A. gazella* than *A. tropicalis*. For example, female pup survival rate for *A. gazella* was 0.27 (95% Credible Interval: 0.22, 0.33), 0.25 (0.15, 0.36) for hybrids, and 0.37 (0.24, 0.54) for *A. tropicalis*. Therefore, despite high rates of hybridisation the slow growth of the population was not linked to differing hybrid survival rates. Rather the population's small numbers in conjunction with predation risk from New Zealand sea lions (*Phocarctos hookeri*), and distance from other breeding colonies were identified as the key factors in the slow population growth rate.

Keywords: Hybrid, genotype, phenotype, survival, *Arctocephalus* spp., mark-recapture, Bayesian

Introduction

Species distribution ranges are shifting in response to anthropogenic changes in the environment (McCarthy and Possingham, 2007; Hoegh-Guldberg *et al.*, 2008; Doak and Morris, 2010; Pecl *et al.*, 2017). A species' ability to successfully establish itself in a new habitat is an important process in meta-population biology, and in our understanding of range expansion, and re-colonisation dynamics. Successful establishment of a species in a new habitat via range expansion or re-colonisation depends on a multitude of factors including: suitable habitat, prey availability, competition, and predation (Moorhouse *et al.*, 2009; Moseby *et al.*, 2012; Soorae, 2016). Rates of successful species colonisation are difficult to ascertain, as there are few empirical free-living system studies. However, a study by Payo-Payo *et al.* (2017) estimated that just over 50% of new bird colonies are successfully established, suggesting there are many barriers to successful new colony establishment for long-lived species.

One of the best examples of successful re-colonisation is in the fur seals (*Arctocephalus* spp.) (Magera *et al.*, 2013). Over-harvesting of fur seals during the commercial sealing period (18th and 19th centuries) led to numerous localised extinctions and near extinction of several species throughout the Southern Ocean. Following the cessation of commercial sealing, the remaining fur seal populations began to recover, and eventually, re-colonise their former breeding sites (Bonner and Laws, 1964; Wynen *et al.*, 2000). The most notable example is the Antarctic fur seal (*Arctocephalus gazella*), whose population was thought to have been eliminated by the end of the 19th century, before its rediscovery in 1907 at South Georgia (Boyd, 1993). The population at South Georgia then increased from "hundreds of animals" in 1933 to 4.5 to 6.2 million in 1999/2000 (Bonner, 1968, Laws, 1973; Boyd, 1993; Hofmeyr *et al.*, 2005). Less heavily exploited than *A. gazella*, the subantarctic fur seal (*Arctocephalus tropicalis*) (Bonner and Laws, 1964) has exhibited similar increasing population trends at its three main breeding sites (Gough Island, Amsterdam Island and the Prince Edward Islands: Marion and Prince Edward Island) where 99% of *A. tropicalis* breed (Bester, 1990; Guinet *et al.*, 1994; Bester *et al.*, 2003). Comparisons of *A. gazella* and *A. tropicalis* population growth rates are comparable at many re-colonised breeding sites in the Southern Ocean (SCAR-EGS, 2008). However, population growth rates of *A. gazella* and *A. tropicalis* are generally lower at Macquarie Island than other breeding sites, which has been attributed to the complex re-colonisation process of three

sympatric species at Macquarie Island and the island's geographic isolation from the major population centres for each species (Goldsworthy *et al.*, 2009).

The original species of fur seal on Macquarie Island was only referred to as the "Upland Seal" (Lesson, 1828), and its true taxonomic status is unknown. It has been hypothesised the "Upland Seal" may have been *A. tropicalis* or juvenile New Zealand fur seals (*Arctocephalus forsteri*) (Shaughnessy and Fletcher, 1987b; Taylor, 1990). However, ancient DNA analysis could not match the "Upland Seal" to either *A. tropicalis* or *A. forsteri*, suggesting the "Upland Seal" may have been a now extinct species (Salis *et al.*, 2016). At the beginning of the commercial sealing era, the 'Upland Seal' population was estimated at approximately 200,000 (Ling, 1999). By 1840 Macquarie Island's native fur seal species was declared extinct, and continuous human presence due to the on-going harvesting of Southern elephant seals (*Mirounga leonina*) and penguins prevented the recovery and re-colonisation by southern fur seals (Mawson, 1943). In 1948, 200 juvenile *A. forsteri* were observed on the island, and in 1955 a pup was sighted with an *A. gazella* mother (Csordas, 1963). Female *A. gazella* numbers continued to grow slowly after 1955, however, male *A. gazella* did not hold breeding territories until the early 1990s (Goldsworthy *et al.*, 2009). Male *A. tropicalis* were regularly sighted at Macquarie Island from the 1950s onwards, and the males were the dominant territory holders, but *A. tropicalis* females did not commence breeding until the early 1980s (Goldsworthy *et al.*, 2009). This situation facilitated high levels of hybridisation. Nonetheless, pup production of both species slowly increased from 1955. Genetic analysis of pups born from 1992 to 2003 revealed 17–30% of all pups were hybrids; (Wynen, 2001; Lancaster *et al.*, 2006), much greater than those observed at other sympatric breeding sites (2-5% at Iles Crozet and Marion Island) (Hofmeyr *et al.*, 2006b; Kingston and Gwilliam, 2007; Bester *et al.*, 2009).

Hybrid pups on Macquarie Island between 1992 and 2003 were most commonly between *A. gazella* and *A. tropicalis* and comprised 60% of all hybrid pups (Lancaster *et al.*, 2006). Most were the result of mating's between *A. gazella* females and *A. tropicalis* males, which was unexpected, given colonisation patterns and the relative number of each species in the breeding population during that time: female *A. gazella* accounted for 69.7% of the population and female *A. tropicalis* 13.6% (Lancaster *et al.*, 2007b). Despite there not being a breeding population of *A. forsteri*, only transiting juvenile and subadult males, 40% of the hybrid pups were found to have *A. forsteri* DNA (Lancaster *et al.*, 2006; Lancaster *et al.*, 2010). The Macquarie Island fur seal population represents the most significant

pinniped hybrid contact zone (Wynen *et al.*, 2000; Lancaster *et al.*, 2006; Goldsworth *et al.*, 2008) and has been slow to recover post-sealing. The extent to which hybridisation may have contributed to the low rate of recovery is therefore of interest and is the focus of this study

As *A. gazella* and *A. tropicalis* belong to the same genus and have similar life history parameters, hybridisation between the two species may not affect survival rates directly (Wickens and York, 1997). However, the three species have very different lactation periods (Repenning, 1975). *Arctocephalus gazella* has a short lactation length of around four months, while *A. tropicalis* and *A. forsteri* have an average lactation period of nine to 11 months (Gentry and Kooyman, 1986; Wickens and York, 1997). Weaning mass is an important component of pinniped pup survival (McMahon *et al.*, 2000; Hall *et al.*, 2001; Chilvers *et al.*, 2007). If lactation period is determined by the mother, and pup growth and development are genetically inherited from both parents, hybrid pups between an *A. gazella* female and an *A. tropicalis* or *A. forsteri* male may have a lower survival rate due to a reduced weaning age and mass (Goldsworthy *et al.* 1999).

Hybrids can be difficult to identify in the field based on morphology alone (Wynen *et al.*, 2001). Comparison of phenotypic and genotypic assignment of 1007 pups born during 1992-2003 at Macquarie Island indicated that *A. gazella* and *A. tropicalis* were correctly identified in 96.6% and 92.4% of cases, respectively. In contrast, only 25.3% of hybrid pups were correctly identified, with 74.7% being misidentified as pure species (Goldsworthy *et al.*, 2009). Therefore, assessing the survival rates of *A. gazella* and *A. tropicalis* using phenotypic assessment to differentiate between pure species and hybrids is unreliable (Kery *et al.*, 2010).

This study presents the first demographic assessment of the age- and sex-specific survival rates of *A. gazella*, *A. tropicalis* and their hybrids at Macquarie Island. Additionally, as a recently re-colonised island with long-term field monitoring, the Macquarie Island population provides a rare opportunity to provide empirical data on re-colonisation dynamics of high trophic predators. Due to a limited sample size (n = 157) the survival rates of *A. forsteri* will not be included in this study.

Therefore, this study aimed to (i) update estimates of population growth rates for Macquarie Island fur seal populations and compare them with other *A. gazella* and *A. tropicalis* populations; (ii) quantify factors such as hybridisation, in particular hybrid

survival rates which may limit population growth rates of the populations; and (iii) examine other potential factors, such as predation, which may limit population growth rates of the populations.

Methods

Study site

Macquarie Island (54°30'° S, 158°57° E) is in the southern Pacific Ocean with the main concentrations of breeding fur seals in the main bays of North Head Peninsula (Secluded Beach, Aerial Cove, and Goat Bay). There is some fine-scale separation of breeding between the two species. *Arctocephalus gazella* breed mostly on open pebble beaches within Secluded Beach and Aerial Cove, while *A. tropicalis* mostly breed on the bouldered beaches of southern Secluded Beach and Goat Bay (Lancaster *et al.*, 2010).

Mark-recapture and phenotypic species identification

Mark-recapture studies were carried out annually between 1986/87 and 2011/12 during the summer and early autumn (November to March). Breeding seasons (November–January) are referred to by the year in which they commenced; *i.e.* the 2000/01 breeding season commenced in November 2000.

Pups were initially identified and matched with their mothers using temporary numbers bleached onto their natal fur in the first weeks after birth. After pupping, any unmarked adults and pups older than one month of age were doubled tagged (Size 1, Dalton Superflexitag), each tag applied to the trailing edge of each fore-flipper. Pups which died prior to being tagged were recorded as dead and never tagged. After 1994, seals were also microchipped with a Radio Frequency Identification (RFID) tag applied under the skin along the midline above the base of the tail, and all RFID tags were tested after insertion to ensure readability by the receiver. The RFID tag allowed for seals that lost both tags to be identified and retagged. During tagging, pups were also sexed and assigned to a species based on an integrated phenotype score that included; colouration and pattern of pelage (Shaughnessy *et al.*, 1988a; Goldsworthy *et al.*, 1997a; Wynen, 2001; Lancaster *et al.*, 2010). Individuals with intermediate phenotype scores were classified as hybrids.

During each field season, tag resights were undertaken daily with the aid of binoculars to reduce disturbance. The presence or absence of tags in each fore-flipper and the corresponding tag number were recorded. At the end of the breeding season, observers could enter the breeding territories, and seals missing one or both tags (identified by the presence of a tag hole/rip in the fore-flipper) were opportunistically scanned for an RFID tag, captured and retagged. If they did not have an RFID tag (tagged before 1994, not microchipped at the time of tagging, or the RFID tag failed), an RFID tag was inserted. Long-term identification of individual seals, which were retagged, was managed by matching and recording a seal's new flipper-tag ID to their original flipper-tag ID and/or their RFID number.

Genotypic species identification

Genetic species assignment of the Macquarie Island fur seal population was carried out by Lancaster (Lancaster, 2007). A full description of DNA extraction and analysis methods are detailed elsewhere (Lancaster *et al.*, 2006; Lancaster *et al.*, 2007a; Lancaster *et al.*, 2007b). An overview of these species assignment is detailed below. Tissue biopsies were collected with a 6 mm biopsy punch from all pups born in the breeding seasons 1992, 1994-96, 1998-99, 2001 and 2003. Skin samples were then stored in salt-saturated 20% dimethyl sulphoxide (DMSO) or 100% ethanol at -20ºC until extraction.

DNA was extracted using 2x cetyltrimethylammonium bromide (CTAB) protocol modified from (Murray and Thompson, 1980). A 417-bp fragment of maternally inherited $tRNA^{thr}$ was amplified using polymerase chain reaction (PCR) utilising the reaction volumes and buffers. A restriction fragment length polymorphism (RFLP) assay to assign pure species to each of the three fur seal species (Wynen *et al.*, 2000) was employed in this mtDNA analysis. Each pup was screened at ten microsatellite loci using the parameters outlined above.

Each pup was assigned to a pure species or hybrid status using their mtDNA RFLP profiles, and the software program STRUCTURE, which probabilistically assigned each pup based on their Q values into their overall species class based on their microsatellite

data (Pritchard *et al.*, 2000) and using extensive microsatellite reference data from both parental species and *A. forsteri* across their geographic ranges.

Small samples of hybrid pups from similar parental matings (*e.g. A. gazella* and *A. tropicalis*) (Table 1) led to unreliable survival estimates with wide credible intervals, providing a poor estimate of the affects of hybridisation on survival. Therefore, hybrid survival was estimated by combining all hybrid types.

Table 1. Species and hybrid composition of pups born at Macquarie Island (1992, 1994-96, 1998-99, 2001 and 2003). Total numbers represent all pups genotypes from 1992 to 2003; based on Lancaster *et al.*, (2006). Number of pups implanted with an RFID tag represents pups born post-1993 which were flipper tagged and implanted with an RFID tag, allowing for future identification and survival analysis. (*A.* denotes *Arctocephalus* genus).

Species and hybrid composition	**Total number of pups of each species and hybrid genotype (*N* = 1007)**	**Number of pups of each species and hybrid genotype implanted with an RFID tag (*n* = 890)**
A. gazella	599	522
A. tropicalis	173	160
A. forsteri	0	0
A. gazella - *A. tropicalis*	141	123
A. gazella - *A. forsteri*	66	59
A. tropicalis - *A. forsteri*	12	11
A. gazella - *A. tropicalis* - *A. forsteri*	16	15

Species composition

Genetic profiles were only available for 1007 fur seal pups sampled over eight breeding seasons (Lancaster *et al.* 2006). Therefore, to present a longer time series of trends in species composition in the populations, we used phenotypic data from all pups and adults species (*A. gazella, A. tropicalis, A. forsteri,* hybrids, and unknown species) in each breeding season over the 26-year period (N = 4319). Previous assessments of phenotypic and genetic data identified that the phenotypic scoring method was reasonably accurate in correctly identifying *A. gazella* (~97% correctly assigned) and *A. tropicalis* pups (~92% correctly assigned), but was poor in identifying hybrids pups (only 25% of pups correctly

assigned) (Goldsworthy *et al.* 2006). Therefore, survival estimates of hybrids could only be modelled using the data of pups identified as hybrids via genotyping.

Pup production

Species-specific trends in pup production and hybridisation rates at Macquarie Island were previously described using 22-years of data (1986–2007) (Goldsworthy *et al.*, 2009). We updated this with an additional four years of data (2008–2011). The low number of pups born each year, ensured pup counts were accurate as they are based on direct counts rather than estimates. Annual total pup counts were based on the number of pups marked (bleached or tagged) plus those known to have been born but not marked (*e.g.* that died before reaching one month of age).

Non-linear population growth rates of *A. gazella* and A. *tropicalis* were fitted to a logistic curve using the log number of pups: $y = A/(1+B.e^{c.x})$, where y is the log number of pups, x is the year and A, B, C are model parameters. Overall mean growth rates were calculated and expressed as a percentage of change in the number of pups between two given years: $(N^{t+n} - N^t)/ N^t \times 100$, where N is the number of pups in a given year (*t*). A logistic curve could not be fit to the hybrids due to the relatively small samples and high inter-annual variability. Therefore, rates of change in hybrid pup numbers (*r*) were calculated using a linear regression of the natural log number and expressed as a percentage: $(e^r - 1) \times 100$ (Caughley, 1977).

Survival Analysis

Survival rates of hybrids were estimated solely using seals identified via genotype assessment ($n = 209$), and annual survival rates of *A. gazella* and *A. tropicalis* were based on seals identified via phenotype assessment. Survival probabilities of seals identified via genotype and phenotype assessment were calculated using a Bayesian multi-event, multi-state model, which accounted for dependent flipper tag loss to reduce survival bias (Schwarz *et al.*, 2012; Chapter Two). The model estimated four parameters; survival probability (Φ), resight-probability (p), probability of losing flipper tags (ψ), and probability of detecting an RFID tag ($\boldsymbol{d}_R$). We assumed RFID tags were a long-term form

of secondary identification with a low likelihood of failing (Smyth and Neble, 2013). However, as the tag loss models do not incorporate RFID tag loss, it is therefore subject to biases that underestimates species survival estimates (Chapter Two). Although our survival estimates may be conservative, any bias caused by RFID tag loss/failure does not confound the overall comparison of the effects of age, sex and/or species on survival rates in this study.

The population was divided into three age classes: pups, juveniles and adults. Pups were classified as being less than one year old; and this age class included pups known to have been born but were never tagged (*e.g.* that died before reaching one month of age). Juvenile *A. gazella* and hybrids were classified as between one to three years of age, while *A. tropicalis* aged between one and four years old were labelled as juveniles (Payne, 1977; Bester, 1987). All remaining animals were classed as adults. Bayesian multi-event, multi-state models based on the standard Cormack-Jolly Seber (CJS) mark-recapture model (Lebreton *et al.*, 2009), were created in the Fortran program MTG (Metropolis within Gibbs) (Schwarz, 2008). MTG is a Markov chain semi-random walk simulation program. Survival parameters were given uniform priors between zero and one. Simulations were set for a rejection rate near 0.7, a sub-sampling (thinning) of one in 50 and a burn-period of 50 for each inference. The resulting lag-1 autocorrelations were < 0.1, and independent chains with different parameter starting values gave indistinguishable results. To verify convergence and stationarity within the final chains, we used the Heidelberger and Welch convergence diagnostic available from the CODA package in R using standard 10% increments and $p \leq 0.05$ (Heidelberger and Welch; 1983, Plummer *et al.*, 2006). Retagging was incorporated into the model through the addition of five special states, which can be matched to the Markovian matrix (Appendix A):

1. Alive, one tag counted then retagged to have two tags, no RFID tag

2. Alive, one tag counted then retagged to have two tags, RFID tag detected

3. Alive, one tag counted then retagged to have two tags, RFID tag not detected

4. Alive, zero tag counted then retagged to have two tags, RFID tag detected

5. Alive, zero tag counted then retagged to have one tags, RFID tag detected

Within a time-step (breeding season) an animal which was retagged would move from one state to another. For example, an animal seen at time *t* with one tag, which was then retagged with an additional tag was recorded as a special state. Then at *t+1* the animal would be recorded as having had two tags and the probability of transitioning from a tagging state would be recorded as $\psi_{2:x}$.

Predation

During the 1996/97 breeding season a subadult New Zealand sea lion (*Phocarctos hookeri*), killed an estimated 43% of the Macquarie Island pup cohort (Robinson *et al.*, 1999). Given the Macquarie Islands small fur seal population's vulnerability to stochastic events, the Macquarie Island monitoring program began observing and recording *P. hookeri*, sightings each year. These sightings also included estimated annual fur seal pup mortality as a result of *P. hookeri* predation and/or rape between 1998 and 2011. Numbers of fur seal pup deaths caused by *P. hookeri* were based on direct observations and the examination of pup carcases. Deaths due to *P. hookeri* were characterised by the pups skins having been turned inside out, while still remaining attached to the skeleton at the skull.

Results

Species composition

Based on phenotype scoring, in 2011 *A. gazella* was the most common fur seal species at Macquarie Island making up 69.4% of the total fur seal numbers (pups, juveniles and adults), followed by *A. tropicalis* (22.0%; Figure 1a). The remaining 8.3% of the population consisted of *A. forsteri* (0.2%), hybrids (7.2%) and individual fur seals whose species could not be identified (1.2%; Figure 1a). Between 1986 and 2011 the numbers and species composition (%) of *A. gazella* increased and plateaued over the 26-year study period, from 23 (30.5%) to 613 (69.4%) of the total resighted animals (Figure 1a; Appendix D). While *A. tropicalis* numbers also increased, with species composition ranging from seven animals (11.05%) to 194 animals (20.0%) from 1986 to 2011 (Appendix E). However, low sample size and low rates of species assignments using phenotypic scoring from 1986 to 1999, primarily with adults (mean 22.2 ± 9.09 (SD)) increased uncertainty of species numbers

before 2000, although, after 1990 this percentage dropped to 3.64% ± 2.20 (SD) (Figure 1a; Appendix F).

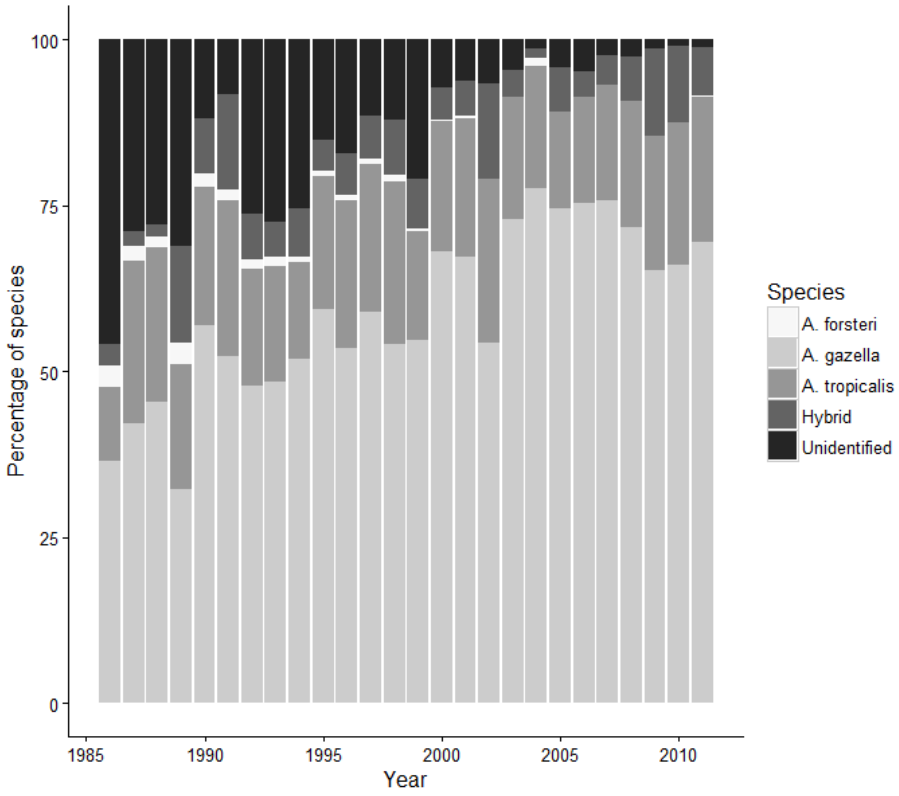

Figure 1a. Species structure of all animals (*Arctocephalus gazella*, *Arctocephalus tropicalis*, *Arctocephalus forsteri*, hybrid fur seals and fur seals whose species could not be identified) tagged as pups and resighted juveniles and adults at Macquarie Island during each breeding season, 1986–2011. Species assignment is based on phenotypic assessment; therefore, hybrids may be misidentified by up to 75% (Goldsworthy *et al.*, 2009).

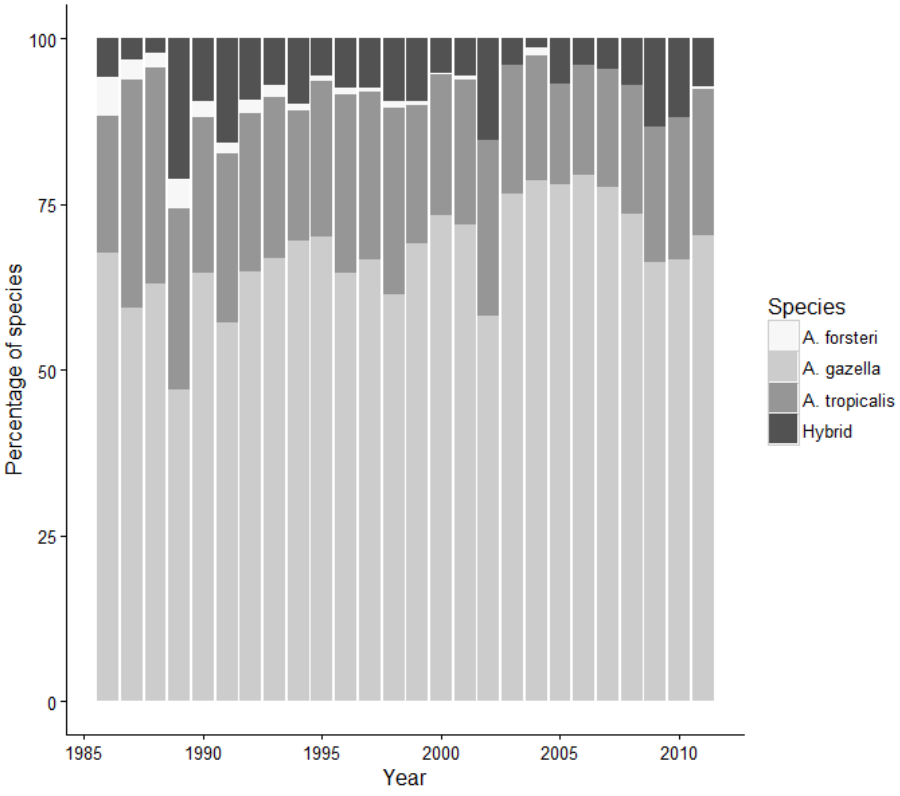

Figure 1b. Species structure of all animals (*Arctocephalus gazella*, *Arctocephalus tropicalis*, *Arctocephalus forsteri,* hybrid fur seals excluding fur seals whose species could not be identified) tagged as pups and resighted juveniles and adults at Macquarie Island during each breeding season, 1986–2011. Species assignment is based on phenotypic assessment; therefore, hybrids may be misidentified by up to 75% (Goldsworthy *et al.*, 2009).

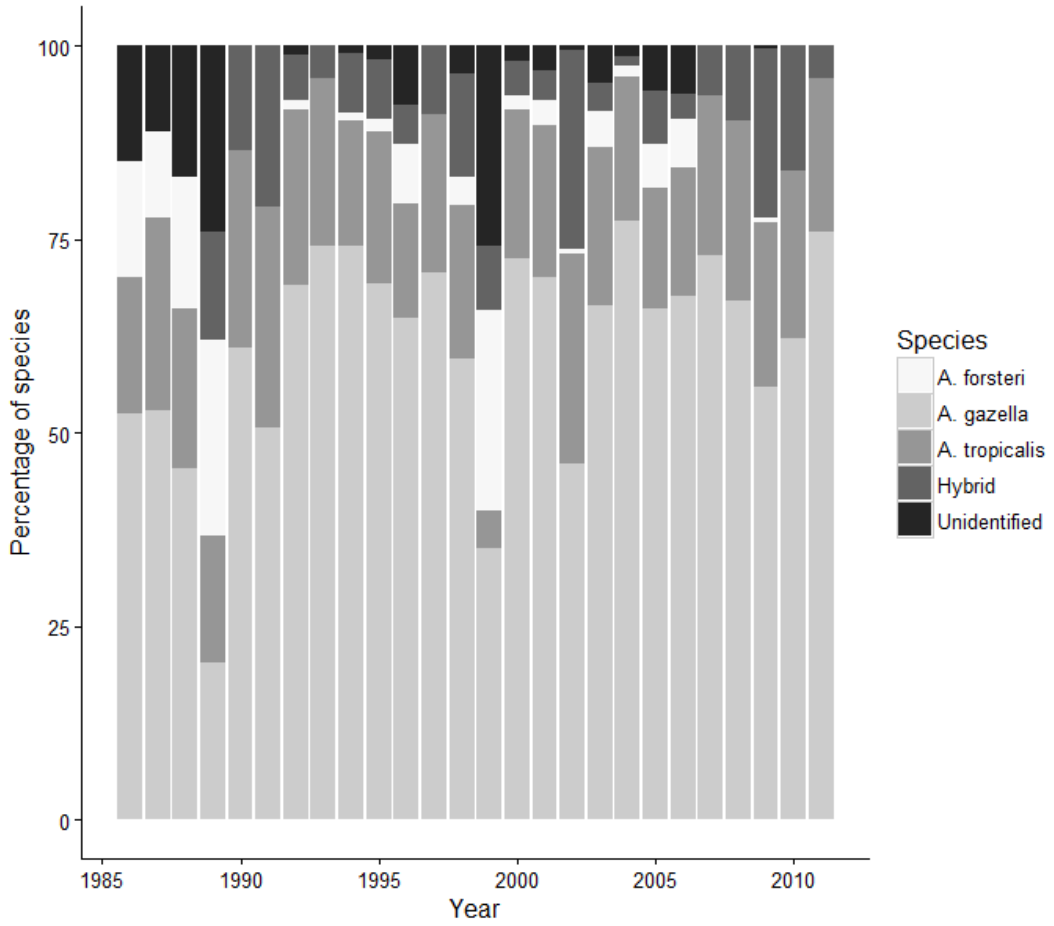

Figure 1c. Species structure of all pups (*Arctocephalus gazella*, *Arctocephalus tropicalis*, *Arctocephalus forsteri,* hybrid fur seals excluding fur seals whose species could not be identified) at Macquarie Island during each breeding season, 1986–2011. Species assignment is based on phenotypic assessment; therefore, hybrids may be misidentified by up to 75% (Goldsworthy *et al.*, 2009).

Pup production

Between 1986 and 2011 (26 breeding seasons) the annual fur seal pup production at Macquarie Island (all species combined) increased from 30 to 248. Based on the phenotypic assessment of pups, *A. gazella* overall mean growth increased significantly at 8.6% per year and shows a plateau trend (Figure 2). In contrast, *A. tropicalis* and hybrids have a much slower rate of increase of pups 3.4% and 4.3% per year respectively and show little indication of plateauing (Figure 2).

The logistic growth curve of *A. gazella*

$$\text{Number of } A.\ gazella = \frac{5.7726}{1+e^{-\text{year}}}$$

The logistic growth curve of *A. tropicalis:*

$$\text{Number of } A.\ tropicalis = \frac{11.0389}{1+e^{-\text{year}}}$$

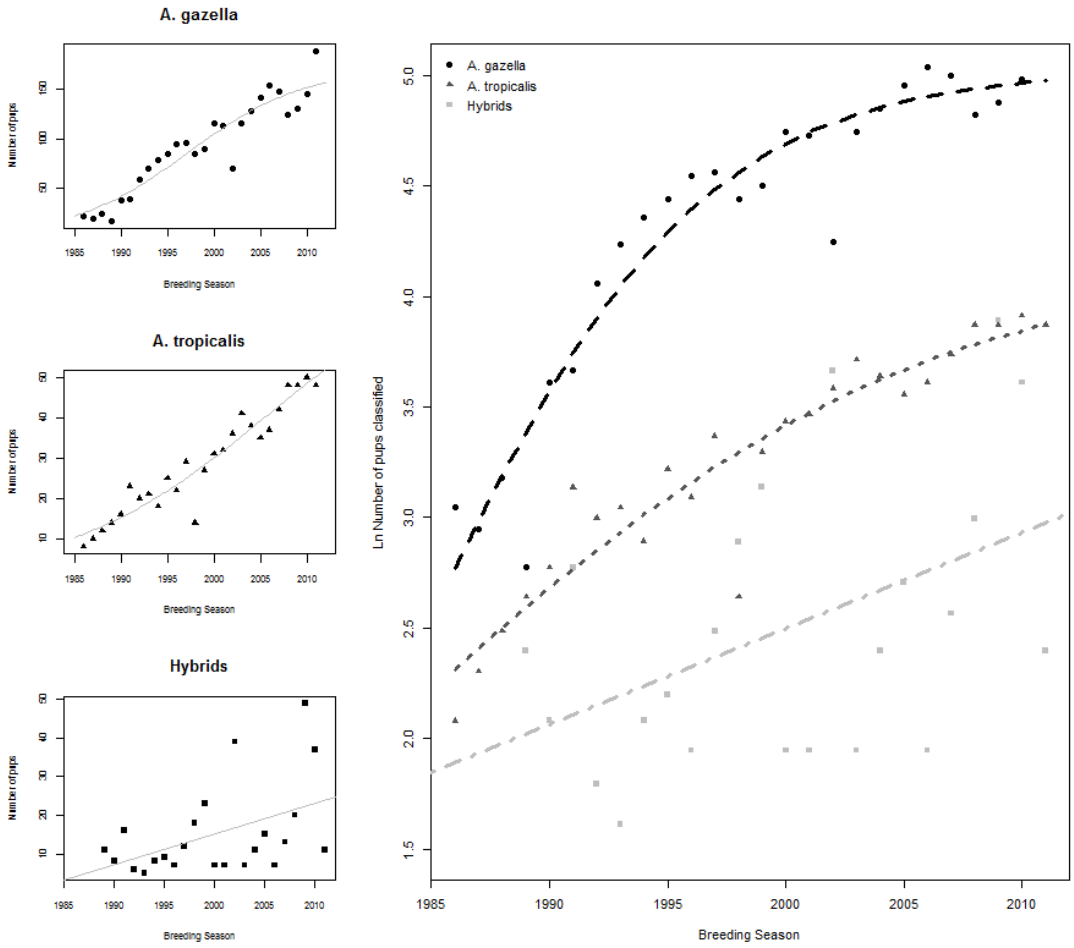

Figure 2. Trends in the number of *Arctocephalus gazella* (8.6% increase), *Arctocephalus tropicalis* (3.4% increase) and hybrid (4.3% increase) fur seal pups at Macquarie Island, 1986/87 and 2011/12, based on phenotypic assessment. Left panel: Number of pups of each species, grey lines represent exponential growth rates for *A. gazella*. and *A. tropicalis*, and linear growth for hybrids. Right panel: Natural log of the number of pups, lines represent logistic growth curves for *A. gazella* and *A. tropicalis* and linear growth for hybrids. Species assignment is based on phenotypic assessment; therefore, *A. gazella* and *A. tropicalis* are accurately identified 96.6% and 92.4% respectively, but hybrids may be misidentified by up to 75% (Goldsworthy *et al.*, 2009).

Survival

Survival Rates Based on Genotype

Accounting for age and sex differences, the posterior distributions of hybrid survival were in the same ranges as *A. gazella* and *A. tropicalis* (Figure 3). Hybrid survival rates more closely resembled the survival rates of *A. gazella* than *A. tropicalis*. For example, female pup survival rate for *A. gazella* was 0.27 (95% Credible Interval: 0.22, 0.33), 0.25 (0.15, 0.36) for hybrids, and 0.37 (0.24, 0.54) for *A. tropicalis*. The small sample size for *A. tropicalis* resulted in wider posterior survival distribution than the *A. gazella* and hybrid species. Pups up to the age of one year had a lower survival rate and greater annual variability than juvenile and adult age classes (Figure 3). For example, the survival rate of female *A. gazella* pups was 0.27 (0.22, 0.33), while female juvenile and adult survival rates of the same species were 0.97 (0.90, 0.99) and 0.93 (0.91, 0.96), respectively. Survival estimates were found to only differ by sex for adult *A. gazella* and hybrids. In both cases, females had higher survival probabilities than males. Female *A. gazella* survival rates (0.93 (0.91, 0.96)) were 9% higher than males (0.84 (0.79, 0.89)), and female hybrid survival rates (0.96 (0.91, 0.99)) were 10% higher than males (0.86 (0.79, 0.92)).

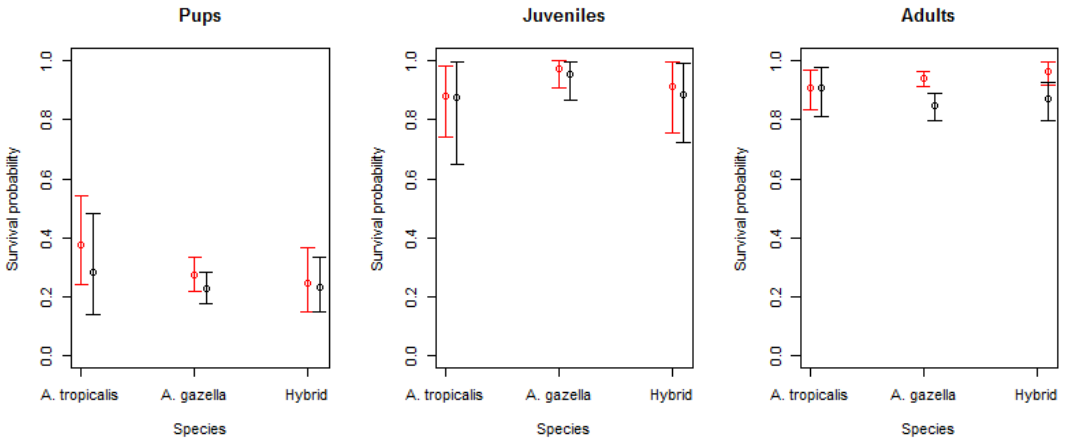

Figure 3. Posterior distribution of estimated survival probabilities as a function of age and sex for *Arctocephalus gazella, Arctocephalus tropicalis,* and hybrid fur seals at Macquarie Island, 1986–2011. Females are red, and males are black. Points are means and bars are 95% credible intervals.

Comparisons of hybrid survival probabilities to *A. gazella* and *A. tropicalis* survival rates were similar enough to one another, that we assumed that any mis-assignments of hybrids based on phenotype would be unlikely to bias overall survival probabilities. As such, we expanded our dataset to include all *A. gazella* and *A. tropicalis* pups born from 1986–2011. A Bayesian survival model using the full phenotypic data set rather than the limited genotype dataset (n = 890) was utilised to quantify the time-varying survival rates of the Macquarie Island *A. gazella* and *A. tropicalis* populations.

Annual Survival Rates Based on Phenotype

Survival analysis grouping of seals by phenotypic assessment found pups had a greater survival variation than juveniles and adults (Figure 4 and Figure 5). For example, annual survival rates of *A. tropicalis* male pups ranged from 0.08 (95% Posterior intervals: 0.002, 0.32) to 0.81 (0.54, 0.99), while male juvenile and adult annual survival rates range were less variable 0.48 (0.02, 0.96) to 0.96 (0.75, 0.99) and 0.49 (0.77, 0.96) to 0.95 (0.84, 0.99) respectively (Figure 4). Although the pup cohorts for *A. gazella* and *A. tropicalis* had similar survival rates, confidence intervals were greater for *A. tropicalis* pups because of the smaller sample size (Figure 4 and Figure 5).

Estimates for survival rates of adult *A. tropicalis* had greater posterior intervals than *A. gazella*, due to differences in sample size. Lower mark-recapture rates (*i.e.* a lower proportion of adults marked) during the early years of the study period resulted in adult survival for *A. gazella* between 1986-1989 (n = 8), and *A. tropicalis* between 1986-1990 (n = 6) posterior survival distributions reflecting the prior distribution. Therefore, there was not enough data to estimate the full 26 years of annual survival probabilities for adults. Furthermore, the apparent increasing trend in adult survival is a result of the decreasing posterior credibility intervals as sample size increases.

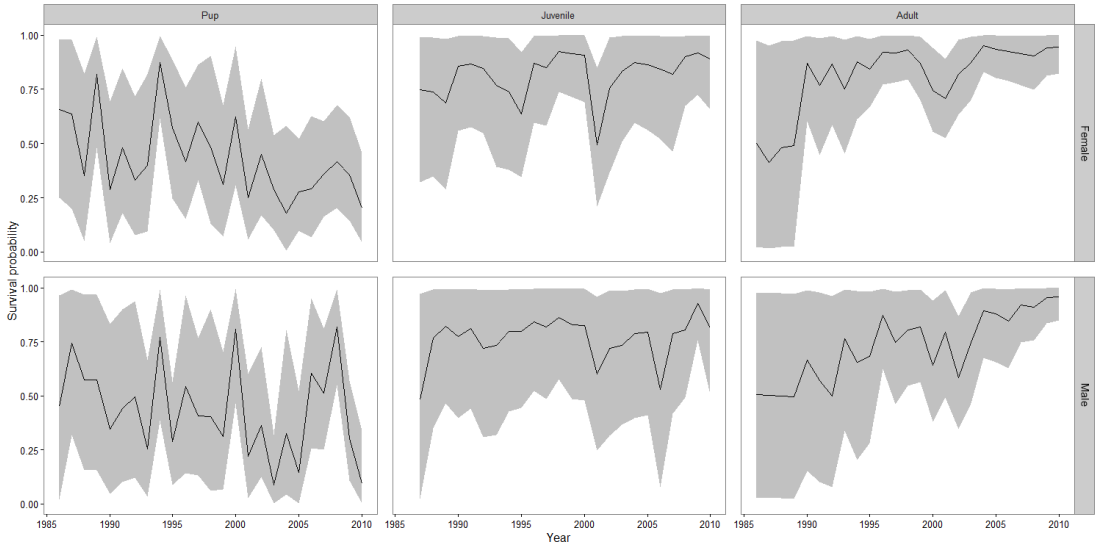

Figure 4. Posterior distributions of annual survivorship estimates of *Arctocephalus tropicalis* at Macquarie Island, 1986–2011, grouped by age class and sex. Black lines represent modelled survivorship. Shaded areas are 95% posterior intervals. Lower mark-recapture rates during the early years of the Macquarie Island fur seal population monitoring program resulted in adult survival for *A. tropicalis* between 1986–1990 posterior survival distributions reflecting the prior distribution due to a small sample size.

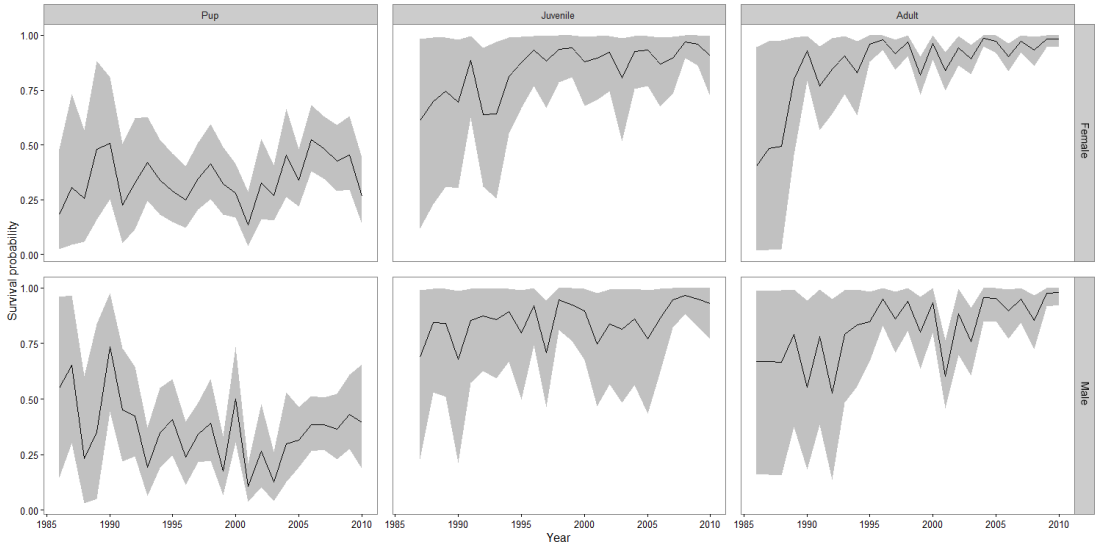

Figure 5. Posterior distributions of annual survivorship estimates of *Arctocephalus gazella* at Macquarie Island, 1986–2011, grouped by age class and sex. Black lines represent modelled survivorship. Shaded areas are 95% posterior intervals. Lower mark-recapture rates during the early years of the Macquarie Island fur seal population monitoring program resulted in adult survival for *A. gazella* between 1986–1989 posterior survival distributions reflecting the prior distribution due to a small sample size.

Predation

Between 1995 and 2011 a varying number (actual numbers were hard to determine as animals were not tagged) of juvenile and adult male *P. hookeri* were observed hauling out at the North Head area of Macquarie Island during the fur seal breeding season. Pup mortality rates due to *P. hookeri* were estimated to range from 0% to 43% between 1994 and 2011 (Table 2).

Predation was not isolated to one or two individuals, with multiple adult and subadult males, some with district markings, being recorded predating on the pups over the 18-year period (1994–2011).

Table 2: Percentages of *Arctocephalus gazella* and *Arctocephalus tropicalis* pups at Macquarie Island killed by *Phocarctos hookeri* between the 1994/95 and 2011/12 breeding season.

Breeding Season	Percentage of pups killed by *P. hookeri* (*n*)	Estimated number of *P. hookeri*	*P. hookeri* linked to pup mortality
1994	0% (0)	At least one	None
1995	3% (4)	At least five	Two subadult males
1996	43% (44)	Unknown	Subadult male with scars on back
1997	0% (0)	Unknown	None
1998	0% (0)	Several	None
1999	1% (1)	Four	Juvenile male
2000	1% (1)	Five	Adult male
2001	10% (16)	Several	Subadult male with #4406 tag*
2002	10% (14)	Several	Two males, one with a #4406 tag
2003	2% (3)	At least four	Unknown
2004	-	-	-
2005	2% (3)	Several	Unknown
2006	2% (3)	Very few	Unknown
2007	3% (6)	At least three	Unknown
2008	1% (1)	Several	Small adult male named "Larry"
2009	3% (7)	Several	Small adult male named "Larry"
2010	0% (0)	Two	None
2011	2% (5)	Three	Subadult male

(-) Breeding season survey not undertake; **P. hookeri* identified as an animal born and tagged on Enderby Island, Auckland Island in 1993

Discussion

Macquarie Island was one of the last fur seal breeding sites to be re-colonised after the commercial sealing era (Table 3 and Table 4). The population growth rate of *A. gazella* and *A. tropicalis* at Macquarie Island have been slow compared to other breeding colonies in the Southern Ocean (Tables 3 and 4), and this has been attributed to the complex re-colonisation history of the Macquarie Island fur seal population and its geographic isolation from the major population centres of *A. gazella* and *A. tropicalis* (Goldsworthy *et al.*, 2009). However, it is difficult to assign the slow growth of the population to a single cause, as there are several likely drivers influencing re-colonisation.

Hybridisation

Differences in re-colonisation timings between male and female fur seals of the three species were likely to have led to high rates of hybridisation during the early stages of colonisation. For example, female *A. gazella* were breeding at Macquarie Island 35 years before male *A. gazella* were observed holding territories and breeding, therefore all pups from female *A. gazella* were hybrids during the early stages of re-colonisation (Lancaster *et al.*, 2006; Goldsworthy *et al.*, 2009). In this study, grouping of all hybrids together, despite the presence in the dataset of hybrids resulting from bi-directional hybridisation across all three species and backcrossed individuals, may have masked differences in pup survival rates of different types of hybrids (*e.g.* with *A. gazella* mothers or with *A. tropicalis* mothers). For example, assuming the length of lactation is determined by the mother, and pup growth and development are genetically inherited from both parents, hybrid pups between an *A. gazella* female and an *A. tropicalis* or *A. forsteri* male may have a lower survival rate due to a reduced weaning age and mass. On the other hand, a hybrid pup between an *A. tropicalis* female and an *A. gazella* or *A. forsteri* male may have a higher survival rate due to an increased weaning age and mass (Goldsworthy *et al.* 1999). Through the grouping of all hybrids, these survival differences may be masked. Therefore, by using a large sample size of genotyped fur seals, a more detailed examination of hybrid pup survival rates can be undertaken. To accurately quantify the full effects of hybridisation on survival rates, it is suggested survival rates between different hybrid crosses (*e.g.* an *A. gazella* mother and *A. tropicalis* father or an *A. tropicalis* mother and *A. gazella* father) be compared. Nonetheless, the results of this study, in combination with a review of the

growth rates of other sympatric populations (Table 3 and Table 4), provides a broad-scale overview on the effects of sympatry and hybridisation on population growth.

Hybridisation between *A. gazella* and *A. tropicalis* occurs at three locations: Iles Crozet, the Prince Edward Islands, and Macquarie Island (Hofmeyr *et al.*, 2006b; Kingston and Gwilliam, 2007; Bester *et al.*, 2009; Goldsworthy *et al.*, 2009). Comparison of population growth rates, (excluding growth rates when the population has reached carrying capacity) at sympatric and allopatric sites were not significantly different (Mann-Whitney U Test, $U = 13$, $n_1 = 13$, $n_2 = 5$, $p = 0.061$; Table 3 and 4). However, Macquarie Island has the highest known percentage of hybrid pups within a population (17-30%) of any sympatric site, and more importantly, hybridisation occurs between three species: *A. gazella*, *A. tropicalis* and *A. forsteri*.

Contrary to our hypothesis that hybrid pups would have a lower survival rate due to substantially different (2.5 times) lactation lengths between *A. gazella* and *A. tropicalis*, hybrids displayed survival probabilities similar to those of both pure species. Female *A. gazella* and *A. tropicalis* at Macquarie Island have similar foraging strategies, pup attendance and milk composition, but the growth rates of *A. gazella* pups are greater than *A. tropicalis* pups (Goldsworthy, 1999; Goldsworthy and Crowley, 1999). These differences in pup growth rates have been attributed to the higher metabolic rate and lower growth efficiencies of *A. tropicalis* (Goldsworthy, 1999). However, a subsequent study on metabolic rates of *A. gazella* pups suggests they have a higher metabolic rate and greater energy expenditure than *A. tropicalis* (Arnould *et al.*, 2003).

Although the mechanisms that underpin the differences in pup growth rates among the species are presently unknown, they have been suggested to involve thyroid hormones (Arnould *et al.*, 2003; Beauplet *et al.*, 2003). As genes controlling thyroid hormones are bi-parentally inherited, hybrid pups with an *A. gazella* mother should still have a lower weaning mass and consequently a lower survival rate (McMahon and Burton, 2005). However, as survival rates of hybrid fur seals are similar to pure species, it seems that pups have some control over weaning age.

It should also be noted that early on all Macquarie Island pups were likely to have been hybrids. As these pups reached recruitment age and bred amongst themselves and with immigrant fur seals, the rate of hybridisation during the early stages of re-colonisation was

inevitably high. Therefore, the Macquarie Island population is a highly interbred and backcrossed population (Shaughnessy *et al.*, 1998; Lancaster *et al.*, 2006; Lancaster *et al.*, 2007b; Goldsworthy *et al.*, 2009) (Appendix G). Thus, *A. gazella*, *A. tropicalis* and hybrid fur seal populations at Macquarie Island will have high genetic admixture which may contribute to similar selective traits between all three populations which promote advantageous physiological or behaviour traits for survival (Abbott *et al.*, 2013).

Even within this brief period of 26-years, a shift in species composition could be identified. The proportion of *A. tropicalis* remains constant at around 20% of the total population species, yet the proportion of *A. gazella* increased from 40-50% to 60-70%. The increase in *A. gazella* may partly be attributed to a decrease in unidentified species, but it is most likely due to a decrease in hybrid numbers (Lancaster *et al.*, 2006). As hybrid survival rates are comparable to pure *A. gazella* and *A. tropicalis* survival rates, the decreasing number of hybrids cannot be attributed to the decreased survival rate of breeding hybrid females. The lower population growth rates observed in breeding areas with hybrids supports the suggestion of assortative mating and high fine-scale species site fidelity acting as reproductive isolating mechanisms, reducing hybridisation (Goldsworthy *et al.*, 1999; Page *et al.*, 2001; Page *et al.*, 2002; Lancaster *et al.*, 2007a; Lancaster *et al.*, 2010). Furthermore, although the reproductive success of male hybrids has been studied, there is uncertainty around the effects of hybridisation on the fecundity of female *A. gazella* and *A. tropicalis* at Macquarie Island. Even though there are known fertile hybrids at Macquarie Island, Haldane's rule states fertility of hybrids and their offspring will reduce over multiple generations, and this may be an important factor in the population's slow population growth (Haldane, 1922; Lancaster *et al.*, 2007a).

Table 3. Population growth rates of *Arctocephalus tropicalis* within the Southern Ocean. Population growth rates based on trends of pup numbers in the study period (Years). Population size and number of pups are given from the final year of the study period. Gough Island is the major population breeding site distance is calculated from.

Location	Population growth (%)	Population size	Number of pups	Years	Years since colonisation†	Distance from major breeding population (km)	Speciation	Predation	Reference
Macquarie Island*	3.4	194	47	1986-11	5 - 30	9415	Sympatric	*Phocarctos hookeri*	
Prince Edwards Island*	9.3	~ 150,000	14,130	2001-08	70 - 77	3870	Sympatric	-	(Kerley, 1987; Bester *et al.*, 2009)
	9.5	-	14,465	1987-01	56 - 70				(Bester *et al.*, 2003)
	12.7	-	4,186	1982-87	51 - 56				(Bester *et al.*, 2003)
	10.5	-	-	1952-75	21 - 44				(Condy, 1978)
Gough Island	8.4	-	55,187	1988-05	-	-	Allopatric	-	(Bester, 1987; Bester *et al.*, 2006)
	15.9	-	-	1955-77	-				(Bester, 1977 as in Roux, 1987)
	8.9	-	-	Pre 1955	-				(Bester, 1980; Roux, 1987)
Îles Crozet* (Île de Possession)	19.2	-	190	1978-91	-	4879	Sympatric	-	(Guinet *et al.*, 1994)
Marion Island*	- 46.0	-	8,321	2010-13	79 - 82	3852	Sympatric	-	(Kerley, 1987; Wege *et al.*, 2016)
	5.3	77,018	16,045	1995-04	64 - 73				(Hofmeyr *et al.*, 2006b)
	1.8	49,523	10,137	1989-94	58 - 63				(Hofmeyr *et al.*, 1997)
Amsterdam Island	0.4	-	6414	1982-93	30 - 41	7231	Allopatric	-	(Guinet *et al.*, 1994)
	16.6	-	-	1970-82	18 - 30				(Roux, 1987)
	7.9	-	-	1956-70	4 -18				(Roux, 1987)
St Paul Island	19	-	365	1985-93	-	7203	Allopatric	-	(Guinet *et al.*, 1994)

* Hybridisation occurs within these sympatric populations. †Year of re-colonisation: Macquarie Island (1981), Prince Edwards Islands (1931), Amsterdam Island (1952)

Table 4. Population growth rates of *Arctocephalus gazella* within the Southern Ocean. Population growth rates based on trends of pup numbers in the study period (Years). Population size and number of pups are given from the final year of the study period. South Georgia is the major population breeding site distance is calculated from.

Location	Population growth (%)	Population size	Number of pups	Years	Years since colonisation†	Distance from major breeding population (km)	Speciation	Predation	Reference
Macquarie Island*	8.6	613	184	1986-11	5 - 30	7816	Sympatric	*Phocarctos hookeri*	
Marion Island*	4.0	-	1,533	2010-13	79 - 82	5062	Sympatric	-	(Kerley, 1987; Wege *et al.*, 2016)
	17.1	3644	759	1995-04	64 - 73				(Hofmeyr *et al.*, 2006b)
Prince Edwards Island*	11.4	~ 5280	330	2001-08	70 - 77	5091	Sympatric	-	(Kerley, 1987; Bester *et al.*, 2009)
	16.2	~ 2000	187	1987-01	56 -70				(Bester *et al.*, 2003)
Nyrøysa	0.04	66,128	15,523	1997-01	-	2553	Allopatric	-	(Hofmeyr *et al.*, 2005)
	30.6	65,983	15,489	1989-96	-				(Hofmeyr *et al.*, 2005)
	7.0	-	-	1978-89	-				(Hofmeyr *et al.*, 2005)
	12.4	4000	-	1964-78	-				(McCann and Doidge, 1987; Hofmeyr *et al.*, 2005)
Heard Island	12	~ 4,100	1,012	1986-01	39 - 54	6454	Allopatric		(Shaughnessy, 1988b; Page *et al.*, 2003)
	20	-	172	1962-86	15 - 39				(Shaughnessy, 1993)
Bird Island (South Georgia)	10.7	-	719	1983-92	76 - 85	-	Allopatric	-	(Boyd, 1993; Boyd *et al.*, 1995)
South Georgia	14.0	~ 6.200,000	-	1991-00	84 - 93	-	Allopatric	-	(SCAR-GSS, 2000)
	-9.8	~2,700,00	~ 600,00	1976-90	69 - 83				(Boyd, 1993)
	14.5	-	~ 90,000	1972-75	65 - 68				(Payne, 1977)
	16.8	-	~ 60,00	1957-72	50 - 65				(Payne, 1977)
Cape Shirreff (South Shetland Island)	4.6	14,842	8,577	1992-02	33 - 43	1655	Allopatric	*Hydrurga leptonyx*	(Aguayo, 1970; Hucke-Gaete *et al.*, 2004)

	14	-	5,313	1986-92	27 - 33				(SCAR-EGS, 2008)
Elephant Island (South Shetland Island)	3.8	-	~ 4500	1986-93	27 - 34	1322	Allopatric	*H. leptonyx*	(Aguayo, 1970; Boveng *et al.*, 1998)
Seal Island (North Annex colony)	24.0	-	70	1986-94	27 -35	1321	Allopatric	-	(Aguayo, 1970; Boveng *et al.*, 1998)
Seal Island (North Cove colony)	- 4.2	-	217	1986-94	27- 35			*H. leptonyx*	(Boveng *et al.*, 1998)
Îles Crozet* (Île de Possession)	17.4	-	67	1983-92	-	5895	Sympatric	-	(Guinet *et al.*, 1994)

* Hybridisation occurs within these sympatric populations. †Year of re-colonisation: Macquarie Island (1981), Prince Edwards Islands (1931), Heard Island (1947), South Georgia Islands (1907), South Shetland Islands (1959).

Distance

Macquarie Island represents one of the most isolated breeding populations of *A. tropicalis* and *A. gazella*. Macquarie Island is 6200 km from the nearest other breeding population of *A. tropicalis* (Ille Amsterdam) and 5200 km from the nearest *A. gazella* population (Heard Island), and is the furthest breeding colony from the major breeding population of both species (Table 3 and Table 4). The maximum distance *A. gazella* is documented to travel is over 1200 km, and for *A. tropicalis* the maximum travel distance is 2700 km (Bester, 1989; Arthur *et al.*, 2015). The distance between Macquarie Island and other fur seal breeding colonies, coupled with the dispersal capabilities of fur seals has likely resulted in relatively low immigration rates at Macquarie Island compared to other sites re-colonised post-sealing that were much closer to the major population centres (Table 3 and Table 4). Furthermore, the re-colonisation of Macquarie Island relied on the other more distant breeding colonies recovering to a level that facilitated a level of migration that could establish a breeding population at Macquarie Island (Roux, 1987). This low immigration rate of *A. tropicalis* and *A. gazella* led to a longer than average re-colonisation phase, characterised by few breeding individuals and possible low reproductive rates due to hybrid reproductive isolating mechanisms, causing a slow rate of population growth (Roux, 1987, Lancaster *et al.*, 2007a, Lancaster *et al.*, 2010).

Life history

Species with K-selected life history traits (*e.g.* late maturity, low fecundity and low growth rates will) generally have slower population growth rates than species with r-selected life history traits (Stearns, 1992; Roff, 1993). As a result of female *A. gazella* breeding two years earlier than female *A. tropicalis*, *A. gazella* have a shorter generation time of 9.1 years compared to 10.7 years for *A. tropicalis* (Pacifici *et al.*, 2013). Because of *A. gazella*'s early breeding and shorter generation time, the Macquarie Island population may have contributed to *A. gazella* having a higher population growth and greater re-colonisation success (*i.e.* currently in the establishment phase of re-colonisation: annual rate of increase of less than 10%; Roux, 1987) than *A. tropicalis*, which is still in the survival phase of re-colonisation (annual rate of increase of less than 5%; Roux, 1987).

However, the slow rate of increase and plateauing of pup numbers is most likely just staggered re-colonisation starts which reflects the combined factors (distance, episodic

migration rates, hybridisation and potential low fecundity of hybrids, environmental variation) that have underpinned low intrinsic growth and a recovery that has depended largely on low and, until recently, variable migration. It is hypothesised when the pup production reaches 500 and greater (the proposed minimum population size needed to ensure the long-term survival (Franklin 1980), the intrinsic growth rate of the population will increase, and growth rates will increase to 15% or more as seen at Amsterdam and Prince Edward Island (Table 3); assuming extrinsic factors such as environmental variability and prey availability are favourable for population growth.

Environmental changes

Environmental variation has been identified as one of the most important determinant of sub-adult survival and population growth rates for many species, including *A. gazella* and *A. tropicalis* (Department of Environment and Heritage, 2004; Jenouvrier *et al.*, 2005; McMahon and Burton, 2005; Siniff *et al.*, 2008; Oosthuizen *et al.*, 2016). Multi-decadal observations from the Southern Ocean indicate water temperatures are increasing, circumpolar currents are shifting poleward, and the frequency of extreme events are also increasing (Gille, 2002, Marshall; 2003; Sarmiento *et al.*, 2004). Macquarie Island has experienced a marked shift in climate, such as decreasing sea level pressure and increasing wind speed (Adam, 2009), which reflects the changes observed in the Southern Ocean.

Modelling the Macquarie Island *A. gazella* and *A. tropicalis* responses to climate variability should be undertaken to estimate the effect size that population growth is limited by environmental stressors. But, given the small numbers of *A. gazella* and *A. tropicalis* at Macquarie Island, it can be speculated changes in the sub-adult survival rates, due to environmental variation would lead to a substantial reduction in the annual growth rate of the whole population, due to the population's vulnerability to stochastic events.

Competition

In the 19th century, Macquarie Island supported an estimated population of ~200,000 "Upland Seals" (Richards, 1994). This suggests the foraging areas around Macquarie

Island may be capable of supporting current and future population growth, although not necessarily to the same extent as the previous century. This ecosystem's ability to support a large population may be attributed to the island's location. Macquarie Island lies on the Macquarie Ridge, which is a major obstacle to the flow of the Antarctic Circumpolar Current. Eighty kilometres north of Macquarie Island, where both species forage, there is a 50 km gap in the Macquarie ridge which creates an upwelling of nutrients, supporting a high biomass of Myctophidae, in particular, *Electrona* spp. the main prey item of *A. gazella* and *A. tropicalis* at Macquarie Island (Goldsworthy *et al.*, 1997b; Flynn and Williams, 2012; Rintoul *et al.*, 2014). The high biomass of Myctophids can support both species; as evidenced by their similar foraging locations, behaviour and comparable survival rates between species in all age classes (Goldsworthy *et al.*, 1997b; Robinson *et al.*, 2002). Unfortunately, with no information on the diet of *A. forsteri* at Macquarie Island, it is hard to ascertain if there is direct competition for prey resources between *A. gazella, A. tropicalis* and *A. forsteri.*

In addition to *A. gazella*, *A. tropicalis* and *A. forsteri*, Macquarie Island hosts a diverse range of additional pinniped species: *M. leonina* and *P. hookeri*, and sea bird species; King penguins (*Aptenodytes patagonicus*), Royal penguins (*Eudyptes schlegeli*), Gentoo penguins, (*Pygoscelis papua*), Southern Rockhopper penguins (*Eudyptes chrysocome*), and Black-browed albatrosses (*Thalassarche melanophrys*). Several of these species are migratory and forage away from Macquarie Island limiting the opportunity for competition (Terauds, 2002; Hindell *et al.*, 2003). The central place foraging species such as *E. schlegeli, E. chrysocome* and *A. patagonicus* forage south of foraging areas utilised by *A. gazella* and *A. tropicalis* (Hull, 1999; Wienecke and Robertson, 2002). The majority of diet of *E. schlegeli and E. chrysocome* is composed of krill and other fish species (*e.g. Krefftichthys anderssoni*), reducing the direct competition (Hull *et al.*, 1997). *Aptenodytes patagonicus* diet is dominated by the lanternfish *Electrona calsbergi* and *K. anderssoni,* in contrast to *A. gazella* and *A. tropicalis* which take predominantly *E. subaspera* (Hindell, 1988; Goldsworthy *et al.*, 1997b). Given the different foraging areas and key species prey, competition between *A. patagonicus and A. gazella* and *A. tropicalis* may be limited. Finally, the waters within a 200 nautical mile radius of the island are protected under Tasmanian and Commonwealth legislation restricting fisheries. While fishery targeting the Patagonian toothfish (*Dissostichus elegenoides*) occurs around Macquarie Island there is no dietary overlap (less than 0.1%) between *A. gazella* and *A. tropicalis* prey and commercial fisheries species, therefore, there is little chance of

competition and/or interactions with commercial fisheries (Goldsworthy *et al.*, 2001; Service, 2006).

Predation

Demographic stochasticity dictates that predation is likely an important determinant of population growth rates and re-colonisation successes for re-colonising or re-introduced species, as low population numbers are more likely to be affected by sudden adverse events (Lande, 1993; Palamara *et al.*, 2013).

In 1997 predation by *P. hookeri* resulted in 43% of pup mortality of that years young (Robinson *et al.*, 1999). Although never this high again, *A. gazella* and *A. tropicalis* pups were still killed by various adult and subadult *P. hookeri*, with pup mortality rates rising to 10% on occasion, and averaging 3% per annum between 1994-2011 (excluding the 1997 outliner of 43%), indicating the predation of pups was not a one-off opportunistic event (Table 2). This may account for Macquarie Island *A. gazella* and *A. tropicalis* population having lower establishing and stabilising population growth rates compared to *A. gazella* and *A. tropicalis* at other colonies (Table 2). Furthermore, the high mortality rate caused by predation may account for Macquarie Island *A. gazella* and *A. tropicalis* pups having lower survival rates (23% to 27% and 28% to 37%, respectively) compared to *A. gazella* at South Georgia (76.1% to 83%; Payne, 1977; Boyd *et al.*, 1995), and *A. tropicalis* at Amsterdam Island (67.7%; Chambellant *et al.*, 2003).

The notion that predation limits population growth of establishing populations is further supported by the *A. gazella* populations at Cape Sherriff, Seal Island and regions of the South Shetland Islands, which are subject to predation by leopard seals (*Hydrurga leptonyx*). The population growth rates at establishing colonies with predation are significantly lower than those without (mean 6.16% vs 16.7%, t-test: $t = 2.96$, $df = 7.08$, $p = 0.02$; Table 3). While no studies have accurately quantified the demographic impacts of predation, recent research highlights the vulnerability of small populations to stochastic events with 50% of new sea bird colonies failing due to predation (Payo-Payo *et al.*, 2017).

Conclusion

A complex array of top-down and bottom-up factors determines a species' ability to establish itself in a new environment, whether via re-colonisation or re-introduction. The re-colonisation of Macquarie Island by fur seals has been slow and complex due to its isolation, asymmetric re-colonisation of males and females of each species colonies with inefficient pre-mating isolating mechanisms leading to high levels of hybridisation. While hybridisation was shown to have little effect on individual survival rates of the Macquarie Island population, it should be noted due to the small numbers of genetically identified hybrids, hybrid survival rates were estimated by grouping all hybrid crosses. Through the act of grouping all hybrids together, differences in survival probabilities between hybrid crosses will have been averaged out. Therefore, it is suggested further investigation should be carried out with a larger sample size to explore if there are survival differences between specific hybrid crosses. Furthermore, there is still uncertainty around the effects of hybridisation on fecundity, and the role of predation by *P. hookeri* which may limit population growth, and these are areas of research which warrant future exploration.

Although many factors have contributed to the variable population growth rates of the Macquarie Island population the small population size and high predation risk are the current key factors in the slow population growth rate. As the population of *A. tropicalis* is still in its survival phase and *A. gazella* in the establishment phase of colonisation (Roux, 1987), monitoring of the populations should be resumed until the growth of the population has stabilised, and the likelihood of population failure due to external factors and demographic stochasticity is reduced (Gerber and Hilborn, 2001).

Chapter Four

DIFFERING SURVIVAL RESPONSES TO ENVIRONMENTAL VARIATION BY SYMPATRIC FUR SEALS

D. E. Baird-Bower[1], M. A. Hindell[1], C. R. McMahon[1,2], L. K. Schwarz[3], and S. D. Goldsworthy[4]

[1] Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart Tasmania 7001 Australia
[2] Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman NSW 2088 Australia
[3] Institute of Marine Sciences, University of California Santa Cruz, Long Marine Lab, 115 McAllister Way, Santa Cruz, California 95060 USA
[4] South Australian Research and Development Institute (SARDI). Aquatic Sciences, 2 Hamra Avenue, West Beach, Adelaide, SA 5024 Australia

Abstract

The ability to adapt to shifting ecological niches is an important factor in a species' survival. Behavioural plasticity afforded by a species' life history traits may allow it to respond more rapidly, than inflexible species, to changes in their environment. One method of identifying the importance of 'plastic' life history traits, is to compare the survival rates of sympatric congeneric populations. The sympatric populations of Antarctic (*Arctocephalus gazella*) and subantarctic (*Arctocephalus tropicalis*) fur seals at Macquarie Island provides a unique opportunity to compare the influence of climate on survival. Using a 26-year mark-recapture data set, survival rates were estimated using a Bayesian capture-mark-recapture model in relation to three environmental factors (i) sea level pressure (an indication of the Southern Oscillation Index), (ii) sea surface temperature (SST), and (iii) wind speed. Modelling showed that *A. gazella and A. tropicalis* survival differed by age class, sex and species. Mortality rates were higher for *A. gazella* and *A. tropicalis* pups than adults in relation to all environmental factors. Adult *A. gazella* and *A. tropicalis* displayed different survival responses to increasing sea level pressure and SST. When sea level pressure increased and SST grew warmer, adult *A. gazella* survival probability increased, while adult *A. tropicalis* survival probability remained steady or decreased. As the foraging location and prey of both species are comparable during the breeding season, the differing survival rates between the two species could not be attributed to differing foraging success during the breeding season, but rather differences in the winter migration behaviour. The contrasting responses of survival to climate suggests, as the Southern Ocean warms the *A. gazella* population at Macquarie Island will continue to increase while *A. tropicalis*, which are listed as endangered within Australia territory, are at risk of population decline over time.

Keywords: Life history, sea surface temperature, sea level pressure, wind speed

Introduction

Populations are regulated by intrinsic (*e.g.* age structure) and extrinsic factors (*e.g.* environmental variation) (Sibly and Hone, 2000). Although these factors occur simultaneously, the population dynamics of Southern Ocean marine predators are particularly responsive to ecological factors, as their survival rates are ultimately linked to both the biotic and abiotic aspects of the marine environment (Oosthuizen *et al.*, 2015; Oosthuizen *et al.*, 2016; Clausius *et al.*, 2017). In the Southern Ocean, water temperatures are increasing, circumpolar currents are shifting polewards, and the frequency of extreme events is increasing (Gille, 2002; Marshall, 2003; Sarmiento *et al.*, 2004). These physical forcings are indirectly affecting population growth rates of several species of birds and mammals in the Southern Ocean through changes in prey distribution, abundance, and migration patterns (Sibly and Hone, 2000; Emmerson *et al.*, 2011; Oosthuizen *et al.*, 2016). Although, these physical forcings can also directly effect Southern Ocean predator population dynamics through habitat loss, via reduced sea ice and rising sea levels, and increased storm frequency causing high sub-adult mortality events through exposure and drowning (Learmonth *et al.*, 2006). As such, the decline of many Southern Ocean predator populations have been linked to changing climate conditions such as sea surface temperature (SST), El Niño-Southern Oscillation (ENSO) events and decreasing sea ice-extent (Barbraud and Weimerskirch, 2001; Weimerskirch *et al.*, 2003; Forcada *et al.*, 2005; van den Hoff *et al.*, 2014). Understanding the factors driving population dynamics in response to climate change can be complicated, as species' responses to environmental changes not only depend on what environmental conditions are like but what a species' life history traits are (Forcada *et al.*, 2006).

Life history underpins how species allocate their time and energy in reproduction, development and survival, all of which contribute to population dynamics (Stearns, 1992). For example, animals can maximise their fitness either by maximising reproductive output (r-selected) or survival of offspring (K-selected) (Isaac, 2009). In general, r-selected species produce many offspring and are associated with variable environments, while K-selected species are associated with lower reproductive output and more stable environments (Stearns, 1976). As such, life history traits fundamentally influence how individual survival might be affected by the shifting environmental conditions (Sol *et al.*, 2016). Therefore, when modelling a species response to varying climate, a population's life history traits are important considerations in understanding the factors driving

population changes (Younger *et al.*, 2016). As environmental conditions move away from optimum values for that species, the importance of life history adaptions may become more pronounced (Hoffmann and Sgro, 2011). So, by comparing the survival responses of sympatric populations with different life history traits that occupy the same niche, we can understand the vital role life history traits play in optimising fitness against environmental variability.

Within the Southern Ocean, there are several sympatric populations of Antarctic fur seals (*Arctocephalus gazella*) and subantarctic fur seals (*Arctocephalus tropicalis*): the Prince Edward Islands, Îles Crozet, and Macquarie Island. At Macquarie Island most of the fur seal populations were tagged as part of an annual program that commenced in 1986 and ended in 2011. The intensive tagging effort of the *A. gazella* and *A. tropicalis* populations enabled long-term identification of individuals and the establishment of a known-age population. During the austral summer when the breeding season of both populations overlap, the diet, milk composition, foraging strategies and foraging locations of both adult species are very similar (Goldsworthy, 1999; Goldsworthy and Crowley, 1999; Robinson *et al.*, 2002), but the pups have very different growth rates and growth strategies. As the foraging niche of *A. gazella* and *A. tropicalis* overlap, any contrasting trends in demographic responses to environmental variability may be attributed to their different life history traits. More specifically, differences in foraging plasticity afforded by differing lactation patterns.

While *A. gazella* and *A. tropicalis* belong to the same genus, they have evolved differing lactation strategies (Gentry and Kooyman, 1986). With the major breeding colonies of *A. gazella* being south of the Antarctic Polar Front (APF), *A. gazella* have evolved a brief lactation period of around four months, to utilise the higher prey availability and seasonality of the region to maximise pup survival rates (Gentry and Kooyman, 1986). During lactation *A. gazella* pups gain 76 to 90 g per day (Doidge and Croxall, 1984) (Wickens and York, 1997). In contrast, *A. tropicalis* evolved in the less seasonal, temperate waters north of the APF. These waters are characterised by relatively low but temporally stable resource availability throughout the year. *Arctocephalus tropicalis* have evolved a longer lactation period to enable sufficient energy transfer to pups in this relatively low energy environment (Gentry and Kooyman, 1986), with pups gaining approximately 45 g per day until weaning at around nine to 11 months of age (Goldsworthy, 1999).

Tagging of all pups of both species born at Macquarie Island began in 1986, providing long-term identification of individuals and the establishment of a known-age population.

Using 26-years of mark-recapture data we aimed to i) quantify the survival responses of the two sympatric species to environmental variability, and ii) determine age-specific survival responses of both species to environmental variability. Such information will provide greater insight into the importance of life history trait adaptation to changing environments, which is especially important given the current predictions of global climate change in the forthcoming decades.

Methods

Study population

Macquarie Island (54°30^{o} S, 158°57^{o} E) is located north of the APF and south of the Subantarctic Front. Pups are born from mid-November to early January, with the majority of births occurring in mid-December (Shaughnessy *et al.*, 1988a). From 1986 to 2011 all pups born were captured at one month of age and weighed, sexed and a plastic tag inserted in the trailing edge of each fore-flipper. From 1994, all seals were also marked with a long-term subcutaneous Radio Frequency Identification (RFID) tag on the dorsal mid-line between the pelvis and the base of the tail. Any untagged adults were also marked in this way.

Daily resights of individuals were conducted between November and March of each breeding season from 1986 to 2011, excluding 2004 (breeding seasons designated by the year in which they commenced). Using binoculars, resights were made from the edge of the breeding territories during the breeding season, to reduce disturbances to the seals, and breeding beaches were entered opportunistically post-breeding season to retag seals that had lost tags.

Environmental data

Southern Ocean marine predators are affected by many environmental factors. Due to the relatively small data set and the number of categorical variables required for a full model: age class, sex, and species (n = 6), environmental co-variates were limited to three parameters. Parameter selection was based on environmental variables known to affect Southern Ocean predators and the years of available date of the datasets (Appendix H).

To ensure the full 26-years (1986-2011) of survival data could be utilised, environmental data dating back to 1986 were chosen.

The first parameter was sea level pressure, a local environmental parameter which can be used as an indication of the Southern Oscillation Index (SOI) (Kwok and Comiso, 2002). The SOI is the atmospheric aspect of ENSO. Positive SOI values often indicate La Niña, and are associated with stronger trade winds, cold waters, and higher survival rates of Southern Ocean predators. Negative SOI values are an indication of El Niño, characterised by weaker trade winds and warmer waters, which has been associated with decreased survival rates of Southern Ocean predators (McMahon and Burton, 2005).

The second parameter was another local environmental variable, wind speed. A moderate increase in wind speed is associated with increased ocean mixing and increased nutrients, leading to foraging mass gain of Southern Ocean predators (Dehnhard *et al.*, 2013).

The third environmental variable selected was SST. Sea surface temperature was chosen as a regional environmental variable, because it is known to affect *A. gazella* and *A. tropicalis* population demographics (Georges *et al.*, 2000; Forcada *et al.*, 2005; Oosthuizen *et al.*, 2016).

Currently, there are no winter foraging data for *A. gazella and A. tropicalis* at Macquarie Island, so the analysis was restricted to just the summer months for which there are satellite tracking data. Local environment data: sea level pressure and wind speed from October 1986 to April 2012 were obtained from the Australian Bureau of Metrology (BOM) (Station number: 300004). Sea surface temperature data from October 1986 to April 2012 were obtained from the National Oceanographic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature V2 dataset (NOAA webpage: http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.html). The spatial coverage of the NOAA SST was limited to the potential core foraging areas utilised by *A. gazella* and *A. tropicalis* lactating females, defined as a maximum distance of 226 km from the island (Robinson *et al.*, 2002). To represent the environmental conditions prior to, and during the first five months of the lactation period, daily meteorological data and weekly SST data on a 1° x 1° scale were averaged from November in year *y* to March in year *y+1* to coincide with the breeding season of *A. gazella* and *A. tropicalis*.

Survival Analysis

Daily resights were converted into single annual encounter histories so that an individual seen multiple times throughout the breeding season was recorded as being detected that year. These encounter histories were used in a Bayesian multi-event, multi-state survival model, which accounted for tag loss, to reduce survival bias due to lost tags (Chapter Two; Schwarz *et al.*, 2012). However, as the tag loss models did not incorporate RFID tag loss, it may therefore underestimates survival estimates by a factor of the percentage of seals to lose both tags divided by the probability of an RFID tag failing or being lost (Chapter Two). As RFID tags are considered a long-term form of secondary identification with low likelihood of failing (Smyth and Neble, 2013), this bias was deemed minimal. Retagging was incorporated into the model through the addition of five special states, which can be matched to the Markovian matrix (Appendix A):

1. Alive, one tag counted then retagged to have two tags, no RFID tag

2. Alive, one tag counted then retagged to have two tags, RFID tag detected

3. Alive, one tag counted then retagged to have two tags, RFID tag not detected

4. Alive, zero tag counted then retagged to have two tags, RFID tag detected

5. Alive, zero tag counted then retagged to have one tags, RFID tag detected

Within a time-step (*i.e.* a breeding season) an animal which was retagged would move from one state to another. For example, an animal seen at time *t* with one tag, which was then retagged with an additional tag was recorded as a special state. Then at *t+1* the animal would be recorded as having had two tags and the probability of transitioning from a tagging state would be recorded as $\psi_{2:x}$.

Preliminary analysis found survival rates varied with age and had a high degree of uncertainty, probably reflecting the relatively small sample (cohort) size. To reduce the estimate uncertainty, survival data were estimated for only three age classes: pups, juveniles and adults. Pups were classified as those less than one-year-old. As *A. gazella* and *A. tropicalis* have differing age of sexual maturity, juvenile *A. gazella* were classified as those aged one and three years, and juvenile *A. tropicalis* were one to four years of age (Payne, 1977; Bester, 1987). All remaining animals were classed as adults.

The model included four parameters: survival probability (Φ), resight-probability (p), probability of losing tags (ψ) and probability of detecting RFID tags ($\boldsymbol{d}_R$) (Table 1). Bayesian multi-event, multi-state models based on the standard Cormack-Jolly Seber (CJS) mark-recapture model (Lerreton *et al.* 2009) created in the Fortran program MTG (Metropolis within Gibbs) developed by Daniel Goodman (Schwarz, 2008). The MTG is a Markov chain semi-random walk simulation. Parameters were given uniform priors between zero and one. Simulations were set for a rejection rate near 0.7, a sub-sampling (thinning) of one in 50 and a burn-period of 50 for each inference. The resulting lag-1 autocorrelations were < 0.1, and independent chains with different parameter starting values gave indistinguishable results. To verify convergence and stationarity within the final chains, we used the Heidelberger and Welch convergence diagnostic available from the CODA package in R using standard 10% increments and $p \leq 0.05$ (Heidelberger and Welch, 1983, Plummer *et al.*, 2006).

Table 1. Description of all states for each transition parameter within the Bayesian multi-state multi-event model

Transition parameters	States
Survival probability	Alive, Dead
Resight-probability	Seen, Not seen
Probability of losing tags*	$\psi_{2:2}$, $\psi_{2:1}$, $\psi_{2:0}$, $\psi_{1:1}$, $\psi_{1:0}$
Probability of detecting RFID tags	Detected, Not detected

* ψx:y is the probability of transitioning from x-tag state to y-tag state *e.g.* ψ2:0 is the probability of going from two tags to no tags within a year.

Small sample sizes between 1986-1990 for adults of both species (n = 8 for *A. gazella* and n = 6 for *A. tropicalis*) during the early years (1986 to 1990) resulted in a high degree of uncertainty in survival estimates (as indicated by wide credible intervals). Therefore, there was not enough data to estimate the full 26 years of annual survival probabilities for adults. As such *A. tropicalis* survival data ranged from 1990–2011, and 1989–2011 for *A. gazella*.

All environmental covariates were compared using pair-wise Pearson correlation coefficients to ensure that no inter-correlated variables (cut off: R = 0.50; Table 2) were included in the analysis. Relationships between annual survival rates and environmental

variables were then tested with generalised linear models (GLMs). The GLMs were fitted using 100 random samples from the survival posterior Gaussian distribution, for each cohort and year.

Table 2. Pearson correlation between environmental parameters.

Measure	**1**	**2**	**3**
1. Sea level pressure	-		
2. Sea surface temperature	0.468*	-	
3. Wind speed	-0.072*	-0.006	-

* Correlation is significant at the 0.001 level (2-tailed)

Baseline models including sex, age and species were evaluated first, then the environmental variables were added to the best model. There is a trade-off between increasing model parameters to improve the fit of the model, and overfitting a model thereby obscuring the real underlying model interactions. Model selection was therefore based on the delta Akaike's Information Criterion - corrected (ΔAICc). Here, lower values indicate a more parsimonious model relative to the model fit, models with a ΔAICc less than two are said to have greater support than the other models, ΔAICc values of seven or less have less support, and ΔAICc values greater than ten show no support for the model (Burnham and Anderson, 2004). The Akaike weight, representing the weight of evidence in relation to the top model, was also used to select the best model (Oosthuizen *et al.*, 2016).

Due to the inclusion of age, sex, and species terms within the models, a full model including all environmental variables (sea level pressure, SST, and wind speed), was too complex (with a total of 24 terms including the interactions) to run. We therefore included each environmental covariate separately. While testing the three environmental parameters independently provides information pertaining to the effects of environmental variation on the survival rates of *A. gazella* and *A. tropicalis,* we acknowledged this approach may not fully represent the synergistic nature of the environmental parameters

and may lead to lower correlation coefficients. However, the inclusion of age, sex and species within the model is of greater importance, than the inclusion of all three environmental parameters to understand the effects of environmental variation on the survival and population rates of *A. gazella* and *A. tropicalis*.

Results

In all cases, models with environmental covariates were the better fitting models (Table 3). All baseline models had ΔAICc greater than ten, therefore the baseline models showed sex, age and species did not fully support the underlying survival responses of *A. gazella* and *A. tropicalis* (Table 3). Including age class noticeably increased the log likelihood probability of the data supporting the model, which may indicate survival responses differ by age class, although this is mainly speculation given the high ΔAICc values of the base models.

Mean sea level pressure, SST and wind speed varied considerably across the study period, with minimum and maximum values of sea-level air pressure, SST, and wind speeds reaching: 995.1 hPa and 1003 hPa, 5.314° C and 7.074 °C, and 31.5 km/h and 40.3 km/h respectively (Figure 1). Mean wind speed significantly increased over the 26-year period ($df = 25$, $r = 0.499$, $p = 0.009$), while there was no significant trend of mean sea level pressure and mean SST (Figure 1).

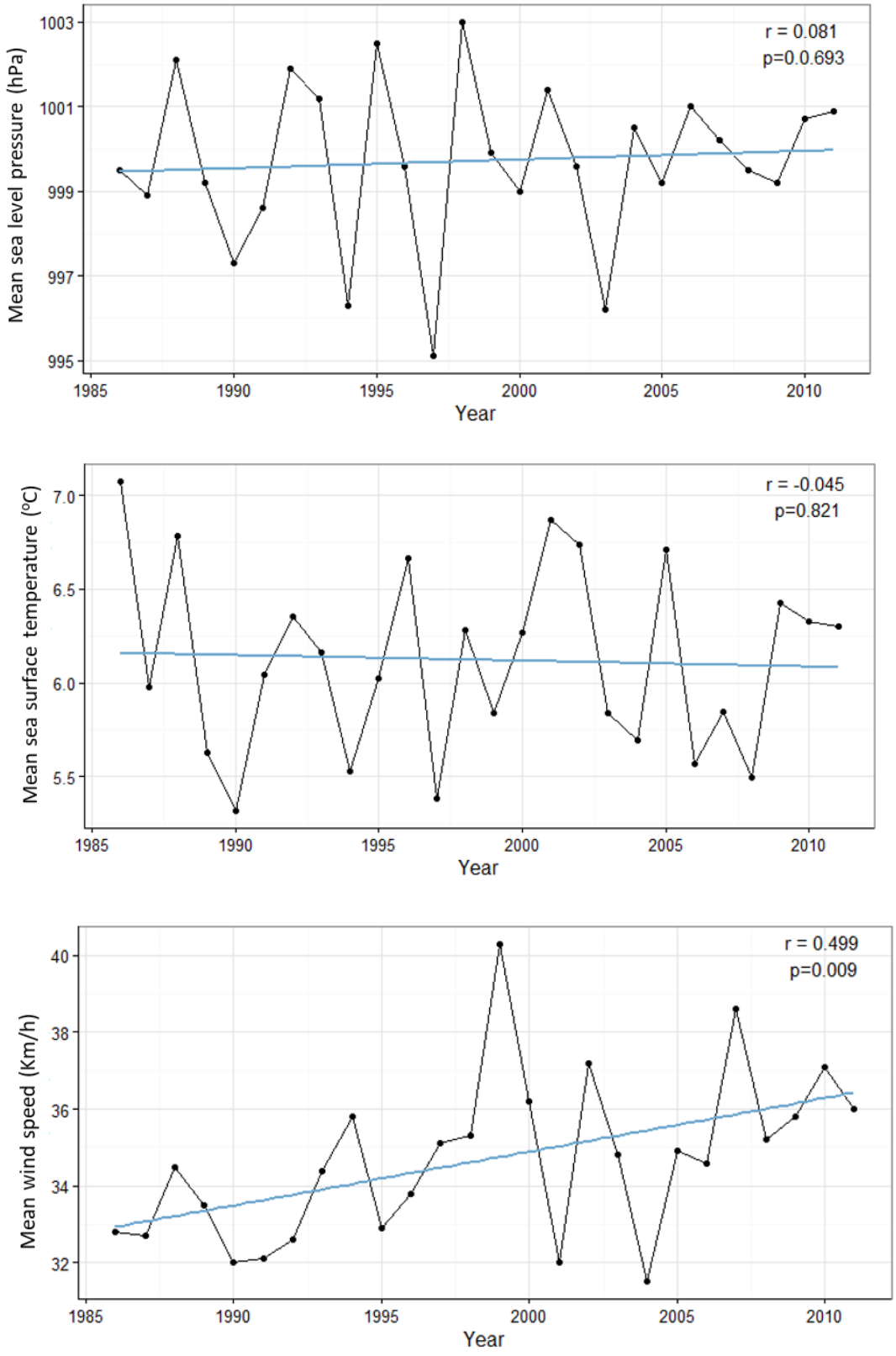

Figure 1. Annual variation of mean sea level pressure (top panel), mean sea surface temperature (middle panel), and mean wind speed (bottom panel) at Macquarie Island (55°5S–53°53.S, 157°5E–160E) from 1986 to 2011. Annual values are means by averaging daily/weekly values from November in year *y* to March in year *y+1*.

Table 3. Selection of models investigating survival responses of *Arctocephalus gazella* and *Arctocephalus tropicalis* to sea level pressure (top), sea surface temperature (SST) (middle) and wind speed (bottom) at Macquarie Island. Model additive effects (+) and interaction terms (*) are described, and the number of parameters (*k*), log of the likelihood, the probability of the data given the model (logLik), AICc, ΔAICc, and Akaike weight (*wi*) are given. Models with the strongest support are highlighted.

	Model	***k***	**logLik**	**AICc**	**ΔAICc**	**wi**
16	Age + Sex + Species: Age*Sex*Species*sea level pressure	13	8010.64	-15995	0	1
8	Age + Sex + Species	5	7244.594	-14479.2	1516.085	0
4	Age + Sex	4	7239.279	-14470.6	1524.714	0
6	Age + Species	4	7160.591	-14313.2	1682.089	0
2	Age	3	7155.308	-14304.6	1690.656	0
7	Sex + Species	4	-4166.83	8341.668	24336.94	0
3	Sex	3	-4170.85	8347.693	24342.96	0
5	Species	3	-4204.29	8414.58	24409.85	0
1	Intercept	2	-4208.29	8420.584	24415.85	0

	Model	***k***	**logLik**	**AICc**	**ΔAICc**	w_i
16	Age + Sex + Species: Age*Sex*Species*Wind Speed	13	8194.672	-16363.3	0	1
8	Age + Sex + Species	5	7244.594	-14479.2	1884.146	0
4	Age + Sex	4	7239.279	-14470.6	1892.775	0
6	Age + Species	4	7160.591	-14313.2	2050.15	0
2	Age	3	7155.308	-14304.6	2058.717	0
7	Sex + Species	4	-4166.83	8341.668	24705	0
3	Sex	3	-4170.85	8347.693	24711.02	0
5	Species	3	-4204.29	8414.58	24777.91	0
1	Intercept	2	-4208.29	8420.584	24783.92	0

	Model	***k***	**logLik**	**AICc**	**ΔAICc**	w_i
16	Age + Sex+ Species: Age*Sex*Species*SST	13	8187.062	-16348.1	0	1
8	Age + Sex +Species	5	7244.594	-14479.2	1868.925	0
4	Age + Sex	4	7239.279	-14470.6	1877.555	0
6	Age + Species	4	7160.591	-14313.2	2034.929	0
2	Age	3	7155.308	-14304.6	2043.496	0
7	Sex + Species	4	-4166.83	8341.668	24689.78	0
3	Sex	3	-4170.85	8347.693	24695.8	0
5	Species	3	-4204.29	8414.58	24762.69	0
1	Intercept	2	-4208.29	8420.584	24768.69	0

Responses to environmental conditions

Sea level pressure

Overall survival rates of adult male and female *A. gazella*, and adult male *A. tropicalis*, were positively correlated with sea level pressure (Table 4 and Figure 2). In contrast, the survival of *A. tropicalis* adult females were negatively correlated to sea level pressure, decreasing 0.6% per hPa increase in sea level pressure.

While the majority of adult *A. gazella* and *A. tropicalis* survival probability increased with increasing sea level pressure, survival rates of pups of both species decreased with increasing sea level pressure (Figure 2). Furthermore, *A. tropicalis* pup survival responses to sea level pressure were more pronounced than that of *A. gazella* pups particularly for females; with *A. tropicalis* pup survival rates decreasing at a rate of 1.1% (males) and 2.9% (females) per hPa increase in sea level pressure, compared to *A. gazella* pups which decreased by 1.1% (males) and by 0.2% (females) per hPa increase in sea level pressure.

Sea surface temperature

Adult male and female *A. gazella* survival rates were positively correlated with SST, with slopes of 1.0% and 0.2% respectively, per 1.0°C increase in SST. In contrast, adult male and female *A. tropicalis* survival rates were negativity correlated with warming SST, but only at a significant level for females, decreasing by 0.6% per 1.0°C increase in SST (Table 5 and Figure 3).

Pup survival in both species were strongly negatively correlated with increasing SST, more so than adults of both species ($df = 1$, $f = 37102.401$, $p > 0.001$). Female *A. gazella* pup survival decreased by 13.0% per 1.0°C increase in SST, while female *A. tropicalis* pup survival rates decreased by 4.5% per 1.0°C increase in SST (Figure 3).

Wind speed

Mean wind speed at Macquarie Island significantly influenced the survival of *A. gazella* and *A. tropicalis* (Table 6 and Figure 4). All adults displayed a moderate positive relationship with wind speed, increasing between 1.3% and 2.5% per 1 km/h increase.

Unlike SST and sea level pressure, the survival responses of males and females to variation in wind speed were similar ($df = 1, f = 11.221$ $p = 0.1882$) as was survival between the two species ($df = 1, f = 11.386,$ $p = 0.3716$).

In contrast to adults, male *A. gazella* pups had a strong negative relationship to increased wind speeds, with survival probability decreasing 1.9% with every 1 km/h increase in wind speed. Survival rates for both sexes of *A. tropicalis* pups decreased in a weak relationship to higher wind speeds (0.4 and 0.3% per 1 km/h) while female *A. gazella* pups and adults of both species responded with higher survival probabilities (Table 6 and Figure 4).

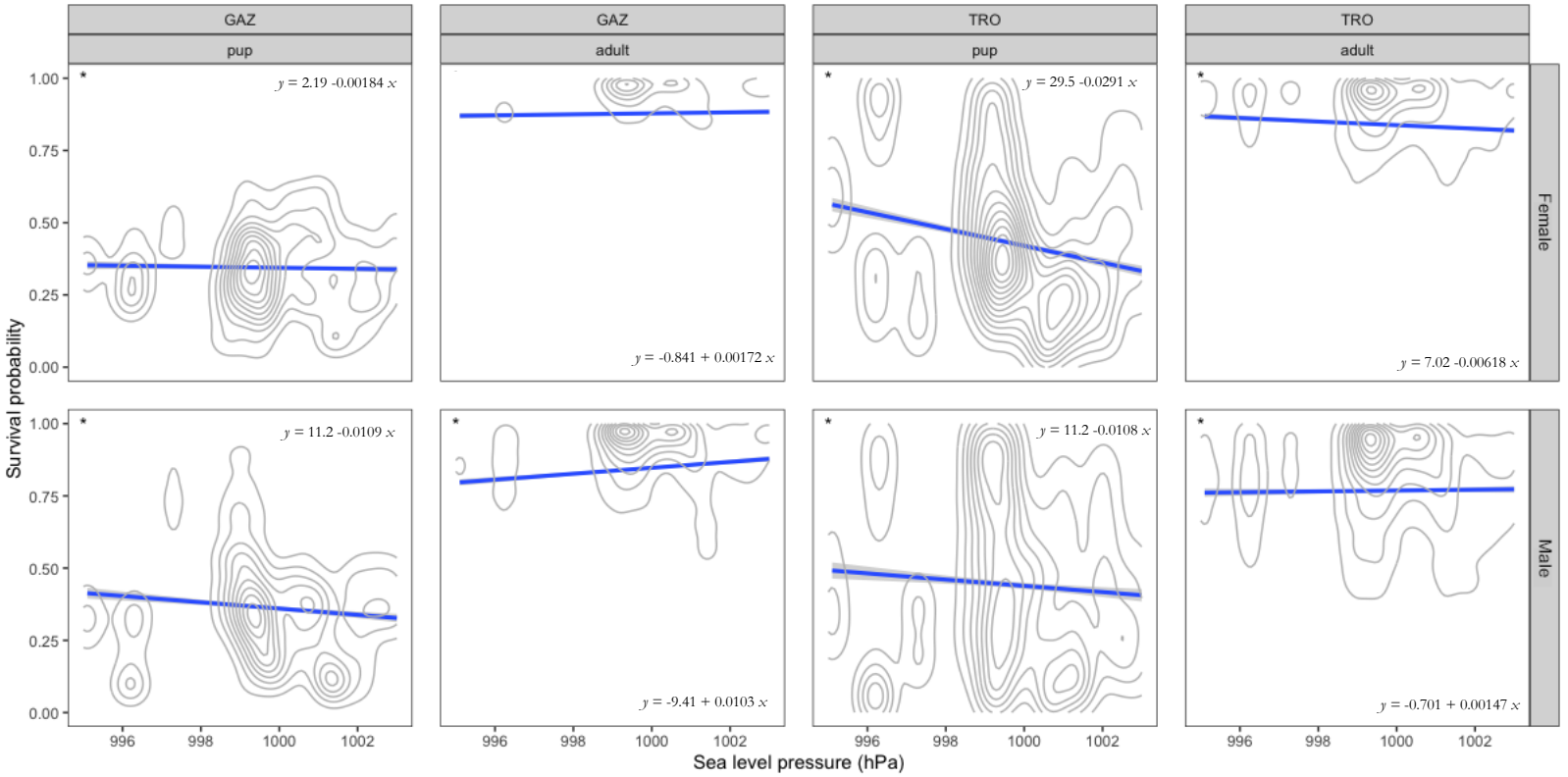

Figure 2. Posterior distributions of survival probabilities of *Arctocephalus gazella* and *Arctocephalus tropicalis* at Macquarie Island as a function of age class, sex, species and sea level pressure. Blue lines correspond to the trajectories of survival in relation to sea level pressure and the narrow shaded areas represent 95% confidence interval. Contour plots correspond to the distribution of the data. Significant coefficeients are shown as in the top left corner *.

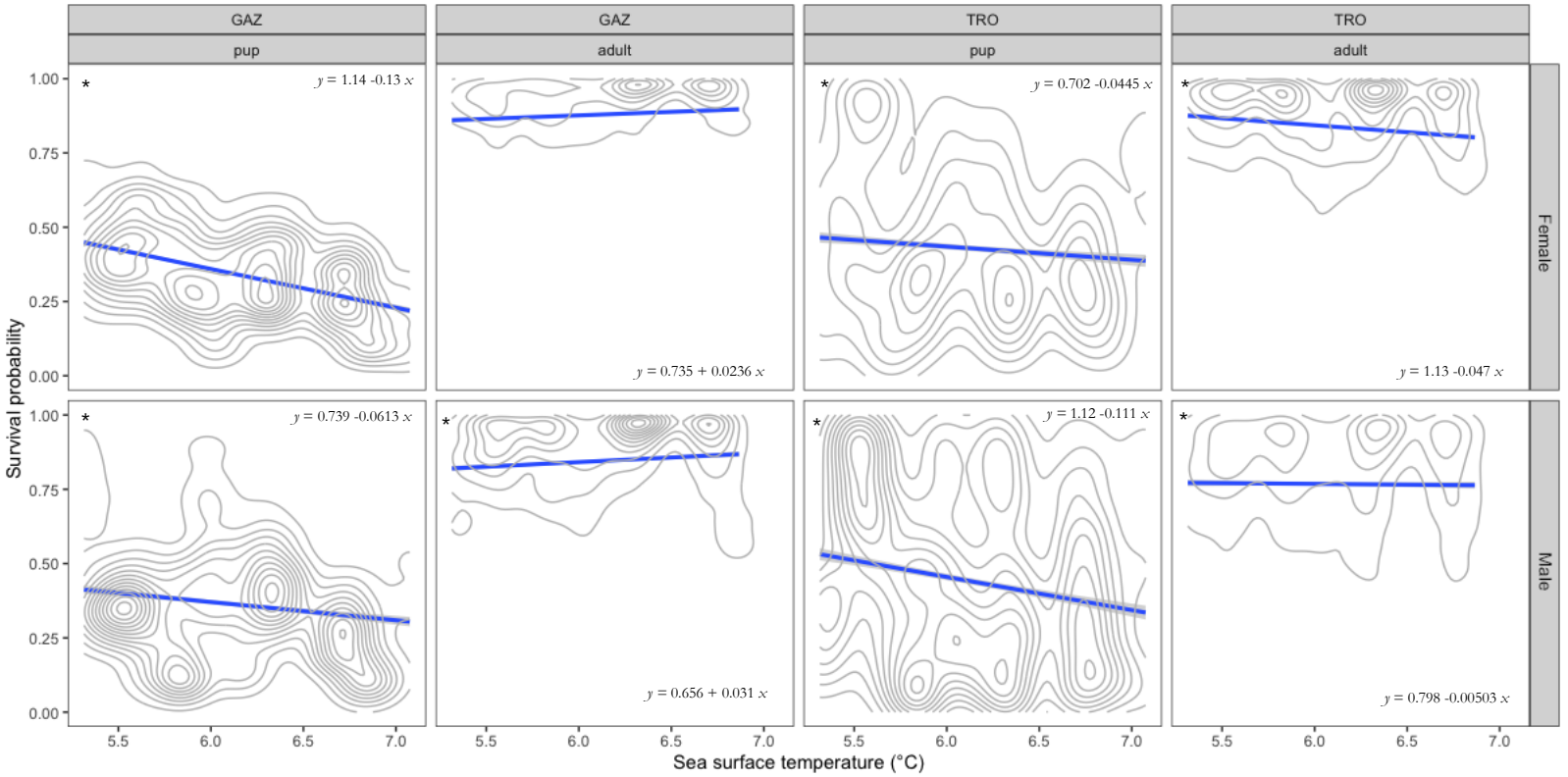

Figure 3. Posterior distributions of survival probabilities of *Arctocephalus gazella* and *Arctocephalus tropicalis* at Macquarie island as a function of age class, sex, species and sea surface temperature. Blue lines correspond to the trajectories of survival in relation to sea surface temperature, and the narrow shaded areas represent 95% confidence intervals. Contour plots correspond to the distribution of the data. Significant coefficeients are shown as in the top left corner *.

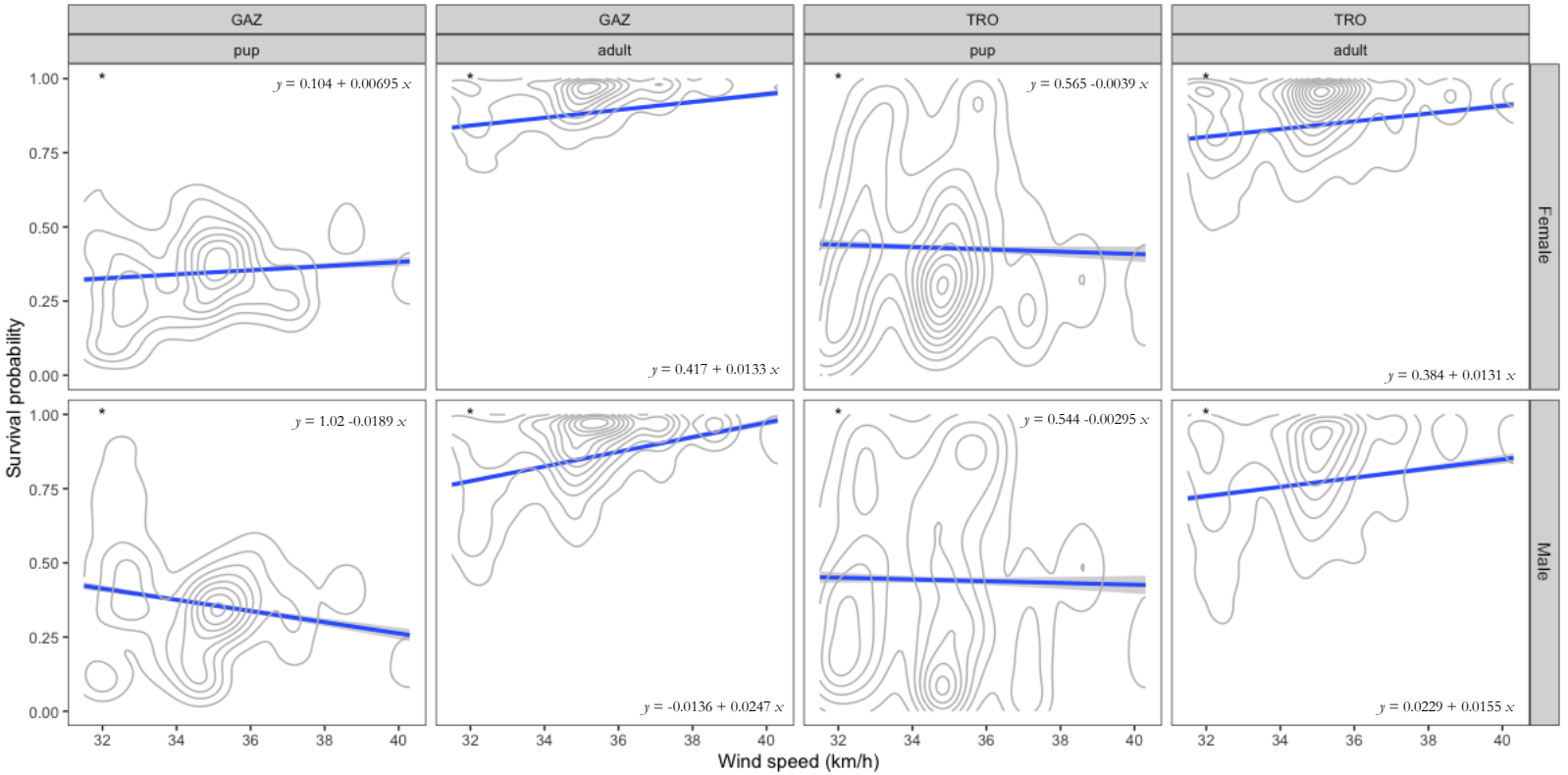

Figure 4. Posterior distributions of survival probabilities of *Arctocephalus gazella* and *Arctocephalus tropicalis* at Macquarie island as a function of age class, sex, species and wind speed. Blue lines correspond to the trajectories of survival in relation to wind speed, and the narrow shaded areas represent 95% confidence intervals. Contour plots correspond to the distribution of the data. Significant coefficeients are shown as in the top left corner *.

Table 4. Summary of *Arctocephalus gazella* and *Arctocephalus tropicalis* cohort survival probabilities at Macquarie Island in relation to top model selection age + sex + species: age*sex*species *sea level pressure. Standard error intervals in parentheses.

Grouping	Correlation with Sea level pressure (*r*)	*p*-values
Female gazella adult	0.003 (0.001)	0.016
Female gazella pup	-0.014 (0.001)	> 0.001
Female tropicalis adult	-0.006 (0.001)	> 0.001
Female tropicalis pup	-0.022 (0.001)	> 0.001
Male gazella adult	0.011 (0.001)	> 0.001
Male gazella pup	-0.006 (0.001)	> 0.001
Male tropicallis adult	0.002 (0.001)	> 0.001
Male tropicalis pup	-0.014 (0.001)	> 0.001

Table 5. Summary of *Arctocephalus gazella* and *Arctocephalus tropicalis* cohort survival probabilities at Macquarie Island in relation to age + sex + species: age*sex*species*sea surface temperature (SST). Standard error intervals in parentheses.

Grouping	Correlation with SST (*r*)	*p*-values
Female gazella adult	0.005 (0.004)	0.209
Female gazella pup	-0.1068 (0.005)	> 0.001
Female tropicalis adult	-0.0169 (0.004)	> 0.001
Female tropicalis pup	-0.1079 (0.005)	> 0.001
Male gazella adult	0.029 (0.004)	> 0.001
Male gazella pup	-0.075 (0.005)	> 0.001
Male tropicallis adult	-0.000 (0.004)	0.948
Male tropicalis pup	-0.0784 (0.005)	> 0.001

Table 6. Summary of *Arctocephalus gazella* and *Arctocephalus tropicalis* cohort survival probabilities at Macquarie island in relation to age + sex + species: age*sex*species*wind speed. Standard error intervals in parentheses.

Grouping	Correlation with Wind speed (*r*)	*p*-values
Female gazella adult	0.017 (> 0.001)	> 0.001
Female gazella pup	0.007 (0.001)	> 0.001
Female tropicalis adult	0.015 (> 0.001)	> 0.001
Female tropicalis pup	-0. 0784 (0.001)	> 0.001
Male gazella adult	0.018 (> 0.001)	> 0.001
Male gazella pup	-0.005 (0.001)	> 0.001
Male tropicallis adult	0.014 (> 0.001)	> 0.001
Male tropicalis pup	-0.005 (0.001)	0.003

Discussion

Species-specific survival responses

Arctocephalus gazella and *A. tropicalis* pups displayed different survival responses to three climate variables over a 26-year period. For both species, pup survival rates decreased in relation to warmer SST and increasing sea level pressure. However, no clear pattern could be determined with regards to pups varying responses by sex and species. For example, female *A. gazella* pup survival rate decreased by 13.0% per 1°C increase in SST, and female *A. tropicalis* survival rate decreased by 4.5% per 1°C increase in SST. Yet, male *A. tropicalis* pup survival rates decreased at a greater rate (11.1%), than male *A. gazella* pups (-6.1%). This suggests additional factors, such as the condition and health of breeding females, in addition to the level of maternal care, may also contribute to pup survival.

Arctocephalus gazella adult survival rates remained stable or increased during periods of warmer SST and lower sea level pressure conditions. In contrast, adult *A. tropicalis* survival rates remained stable or decreased in response to warmer SST and lower sea level pressure conditions; which are associated with low prey availability mediated by lower primary production (Falkowski *et al.*, 1998). Both species forage in an area 30-100 km north of Macquarie Island in the breeding season (Goldsworthy, 1999; Goldsworthy and Crowley, 1999; Robinson *et al.*, 2002), so the differing patterns of survival cannot be attributed to differing foraging successes during the breeding season, but rather to behavioural plasticity afforded by the species' life history traits; in particular, differences in the lactation and winter migration behaviour. *Arctocephalus tropicalis* must remain foraging locally while nursing their pups for around nine to 11 months. In contrast, *A. gazella* are free to range more widely throughout the winter months after their pups are weaned in late summer, enabling them access to more productive waters (Lovenduski and Gruber, 2005; Arthur *et al.*, 2015; Arthur *et al.*, 2017), potentially increasing their foraging success, energy assimilation and physiological condition, prior to the following breeding season and increase their life-time fecundity success (McDonald *et al.*, 2012). Without the constraint of nursing for ten to eleven months, adult *A. gazella* have more time to explore and adapt to shifting ecological niches.

Age-specific survival responses

Pups

As with many Southern Ocean predators, the relationship of survival to environmental factors varied with age (Schwarz, et al, 2013). Pup survival rates of both species were generally lowest during periods of low sea level pressure, warm SST, and higher wind speeds, with the exception of female *A. gazella* pups which showed a marginal increase to increasing wind speeds. As the population dynamics of K-selected species are more influenced by adult survival rates, than juvenile survival rates (Stearns, 1976). *Arctocephalus gazella* and *A. tropicalis* pups survival rates being strong negatively related to SST and sea surface pressure will have a marginal effect on the current population growth rates of the Macquarie Island fur seal population. However, as the effects of environmental variation on the population growth rate of K-selected species are often delayed, the effects of climate change on *A. gazella* and *A. tropicalis* population growth rates may be masked (Saether *et al.*, 2013).

The lower and stable survival rates of three of the four pup groupings (male *A. gazella,* and both sexes of *A. tropicalis*) during periods of increased wind speeds contradicts our hypothesis that survival would be higher when wind speeds were highest. This is because increased wind speed is thought to increase primary production and prey resources by vertical mixing of the surface layers (Dehnhard *et al.*, 2013). There is little research on the effects of wind speed on survival for any marine predator, especially for fur seals (Pelland *et al.*, 2014), therefore it is difficult to reach a single conclusion.

One explanation for this apparent contradiction is that wind speed is positively correlated with the Southern Annular Mode (SAM) (Kidston *et al.*, 2009). During phases of positive SAM indices, chlorophyll concentration in the subantarctic zone decreases due to deeper mixed layer and decreasing light penetration into the water column, thus affecting primary and secondary production (Lovenduski and Gruber, 2005). Newly weaned pups are inexperienced foragers and this naivety may contribute to the lower survival rates in years of low prey resources (*i.e.* high temperatures in the foraging grounds). After weaning, *A. gazella* must learn how to successfully predate, while simultaneously increasing their diving capacities to enable them to forage efficiently (Lowther and Goldsworthy, 2012). This hypothesis is supported by the higher survival rates of *A. tropicalis* in response to higher wind speeds, as they have yet

to become independent foragers during the winter months. Foraging and diving capacities of *A. tropicalis* are allowed more time to develop while still being nursed by their mother for nine to 11 months.

An alternative hypothesis which might explain *A. gazella* and *A. tropicalis* pups' lower survival rates compared to adult is, during periods of increased wind speed there is an increase in storm surges. Strong winds can create large swells, which have been linked to increased mortality rates in pups inhabiting low lying breeding grounds (Anderson *et al.*, 2009), such as those at Macquarie Island. This hypothesis is supported by increased wind speeds increasing adult survival while decreasing pups survival rates.

Adults

In all but one instance, adult *A. gazella* and *A. tropicalis* survival rates in comparison to pup survival rates were less negatively affected by environmental conditions which were associated with a decrease in primary productivity (*i.e.* warmer SST). For example, for every 1°C increase in SST female *A. gazella* pups' survival rates decreased by 13.0%, while female adult *A. gazella* survival rates increased by 2.4% (Appendix I). Although the relationship between periods of low prey resources and fur seal weaning has been well documented (Schwarz *et al.*, 2013; Forcada and Hoffman, 2014; Oosthuizen *et al.*, 2016), the fundamental mechanisms that influence *A. gazellas'* and *A. tropicalis'* foraging behaviour and consequently survival and fecundity rates has not been as well studied as that of Southern elephant seals (*Mirounga leonina*). Using *M. leonina* as an exemplar species; in years when prey resources are low for *M. leonina*, foraging success is lower reducing the energy transfer to weaned pups (McMahon and Burton, 2005), leading to lower pup survival (McMahon *et al.*, 2000; McMahon *et al.*, 2003). However, these conditions have relatively little effect on adult survival rates (Le Boeuf and Crocker, 2005). While *A. gazella* and *A. tropicalis* are income breeders and *M. leonina* are capital breeders, all species are K-selected, and the fundamental principle that juveniles are the age class most sensitive to environmental change, and adult survival rates tend to be stable, holds for all species (Eberhardt, 2002).

Population responses

Both local (sea level pressure and wind speed) and regional (SST) environmental conditions affected adult survival, suggesting that environmental variation is a key driving factor of the population's growth, in addition to many other factors affecting fur seal population growth rates at Macquarie Island (Chapter Three). There is a long-term trend of decreasing sea level pressure and increasing wind speeds at Macquarie Island (Figure 1)(Adams, 2009; Hindell *et al.*, 2012), and the changing environmental conditions may be a factor in the relatively slow recovery rates of the population. Population responses to changes in prey resources due to environmental conditions have been demonstrated for other Southern Ocean predators (*e.g.* Butchart *et al.*, 2010; Hoffmann and Sgro, 2011; Younger *et al.*, 2016; Clausius *et al.*, 2017). Consequently, climate change has been proposed as an impeding or secondary factor limiting the population growth of *A. gazella* and *A. tropicalis* within the Southern Ocean (Hofmeyr, 2015; Hofmeyr, 2016).

Our *a priori* selected environmental factors showed little or no correlation, indicating that sea level pressure, SST and wind speed are independent environmental factors that may act synergistically to enhance or reduce primary production. Of these three environmental factors, SST had the strongest effect on survival rates of *A. gazella* and *A. tropicalis* populations at Macquarie Island. Increasing SST has been shown to positively influence the survival rates of adult *A. gazella*, and negatively affect the survival rates of female *A. tropicalis*. Consequently, as the Southern Ocean slowly warms (Banks and Wood, 2002; Foster and Rahmstorf, 2011), over time, the population growth rate of *A. gazella* at Macquarie Island will increase at a greater rate than *A. tropicalis*.

Conclusion

Although preliminary, our findings indicate that the differences in lactation strategy and the differences in foraging plasticity afforded by the strategies, play an important role in *Arctocephalus* ability to respond to changing environmental factors. Although further data, such as winter foraging movements are required to further support these findings. In conclusion, this study is one of a growing number of empirical studies that demonstrates the importance of behavioural plasticity afforded by a species' life history

traits, allowing species that are more plastic to respond more rapidly than inflexible species to environmental changes.

Chapter Five

DISCUSSION

Research overview

The research objectives of this thesis were to provide an assessment of the potential effects of hybridisation and environmental variation on the recovery of the subantarctic fur seal (*Arctocephalus tropicalis*) and Antarctic fur seal (*Arctocephalus gazella*) populations at Macquarie Island. And to a broader extent to contribute to a body of knowledge regarding intrinsic and extrinsic factors affecting population growth.

Extrinsic factors affecting population dynamics

Environmental variation

Anthropogenic perturbation and environmental variation are the greatest threats to long-term viability for many species (Sala et al, 2000; Walther *et al.*, 2002; Parmesan,

2006). Climate change is the principal force driving many of the observed plant and animal population perturbations that are currently occurring (Thomas *et al.*, 2004). As climatic conditions are currently changing fastest at higher latitudes, Southern Ocean predators may be particularly vulnerable to environmental variation. Understanding how Southern Ocean meso-predators can be effected by oceanographic changes at annual and lifetime scales is challenging, as it requires long-term demographic data, and the migration patterns and diving behaviour of marine mammals make such data difficult to collect (Eberhardt, 1985; Sibly and Hone, 2002; Taylor *et al.*, 2007). However, while many pinnipeds live in remote locations, the logistics of collecting long-term demographic data are feasible, as their site fidelity and the terrestrial phases of their life histories provide an opportunity to collect demographic data over long periods of time (Taylor *et al.*, 2007). Furthermore, as pinnipeds were commercially valuable animals (*e.g.* fur and blubber), there are long-term records available (*e.g.* over 150 years) on the abundance of many species (Poland, 1892; Magera *et al.*, 2013). These historical records provide an opportunity to understand the major factors driving population change on a much longer time scale.

A review on the global threats to pinnipeds, ranked fisheries interactions as the most common threat to red listed species (50.0% of all species), with climate change ranked second (31.8%), followed by hunting (13.6%), then predation (5.6%) (Kovacs *et al.*, 2012). An overview on the effects of major climate change regimes, as identified by the IPCC report (IPCC, 2014), on pinniped fitness found the majority of species were currently not greatly affected by shifting climates (Table 1). In those cases where pinniped species were threatened by climate change, it was primarily due to loss of sea ice, followed by the consequences of extreme climate events such as El Niño (Table 1) (Kovacs *et al.*, 2012). The loss of sea ice is a significant threat for ice-breeding pinnipeds as it is a direct loss of breeding habit. On the other hand, environmental variation can affect individual survival and population growth rates by altering the distribution and abundance of prey resources, therefore, greater uncertainties surround the effects of environmental change on population trajectories (Moore and Huntington, 2008).

A comparison of sympatric *A. gazella* and *A. tropicalis* survival in response to oceanographic change indicated differences in foraging plasticity afforded by differing lactation periods might play an important role in a species' ability to adapt

to shifting environmental factors (Chapter Four). *Arctocephalus gazella* have evolved life history traits to cope with highly seasonal environments. Because they have a short lactation period they can disperse widely in winter, making them better adapted than *A. tropicalis* (with its nine to 11 month lactation period and therefore limited dispersal capacity) to respond to changing environmental factors. Female *A. tropicalis* will be less buffered against environmentally mediated changes in prey availability, due to their restricted foraging range while nursing pups. As climate and oceanographic conditions are changing due to warmer sea surface temperatures and increased frequency of extreme events (Gille, 2002; Marshall, 2003; Sarmiento *et al.*, 2004), *A. gazella* on Macquarie Island may outcompete *A. tropicalis,* making *A. gazella* the 'winners' and *A. tropicalis* the 'losers' of climate change. However, other *A. gazella* populations in the Southern Ocean may not be 'winners' of climate change. A recent ecological risk assessment of polar sea species identified *A. gazella* populations, whose main food supply is Antarctic Krill (*Euphausia superba*), are at risk of decline in the coming decades due to rapid increases in ecosystem fluctuation (Morley *et al.*, 2019).

Predation

Since the end of the 18th and 19th century commercial sealing era, many seal populations have increased significantly. For example, at South Georgia *A. gazella* numbers increased from "virtually extinct" in 1907 to an estimated population size of 6,200,000 in 1999 (Bonner, 1968; SCAR-GSS, 2000). Guadalupe fur seals *(Arctocephalus townsendi*) which were also thought to be extinct in 1917, now have a population total of 17,581 in 2011 (Gerber and Hilborn, 2001; Aurioles-Gamboa, 2015). A comparison of marine mammal recovery rates indicated that pinnipeds have the highest percentage (50%) of species significantly increasing in abundance since exploitation. With the exceptions of flagship species such as polar bears (*Ursus maritimusi*) and sea otters (*Enhydra lutrisi*), which are subject to increased conservation efforts (Magera *et al.*, 2013). However, while pinnipeds have the highest percentage of species' population growth since the end of the commercial sealing era, not all seal populations are displaying the same high rates of population growth. As seal populations which occupy similar environmental niches (*e.g. A. gazella* numbers in the Southern Ocean) are displaying significant variations in population growth rates, it is suggested the factors which limit maximum

population growth are predominantly local factors (*e.g.* competition, predation, or human disturbance) rather than regional factors (*e.g.* climate or environmental variation) (Magera *et al.*, 2013).

Top-down control through predation pressure is known to significantly affects some *A. tropicalis* and *A. gazella* population growth rates (Table 2 and Table 3; Chapter Three). Although population growth rates at Macquarie Island and South Shetland Islands are still increasing, albeit, at a slower rate, levels of predation at Seal Island on the Western Antarctic Peninsula have caused a decline in population trends (Table 3) (Boveng *et al.*, 1998), indicating predation is a site-specific high-risk threat to the recovery of small populations (Palamara *et al.*, 2013).

Other factors

Other extrinsic factors limiting population growth of *A. tropicalis* and *A. gazella* identified by the International Union for Conservation of Nature (IUCN) include: entanglement, tourism, disease, and fisheries interactions (Table 2 and Table 3) (Hofmeyr, 2015; Hofmeyr, 2016). Large populations of *A. tropicalis* and *A. gazella* (*i.e.* Gough Island and South Georgia respectively) may be at a higher risk of future outbreaks from high mortality diseases such as morbillivirus, as warm temperatures and increased density of seals facilitates the spread of diseases (Lavigne and Schmitz, 1990). Due to the isolation from other Southern Ocean populations, the Macquarie Island *A. tropicalis* and *A. gazella* populations are likely to have reduced disease transmission rates when compared with other pinniped populations (Kerry and Riddle, 2009). Nonetheless, warmer temperatures may increase the abundance of bacterial infections and non-bacterial diseases (Patz *et al.*, 1996; Kuiken *et al.*, 2006). Because the primary foraging areas of *A. tropicalis* and *A. gazella* do not typically overlap with fisheries, mortality rates associated with fisheries are low (Goldsworthy *et al.*, 2002). However, in the future, range expansion of Southern Ocean fisheries may increase the frequency of seal interactions in the coming years, excluding populations whose foraging area are within or overlap marine reverses such as the Macquarie Island fur seal population (Hanchet *et al.*, 2003; Hofmeyr, 2016).

Table 1. Overview combined from different sources ranking the severity of major climate change effects on survival or factors relating to survival (*e.g.* weaning mass, breeding habitat) of individual pinniped species. Number severity: 0 no effect; 1 little to no effect; 2 known or assumed decreases in fitness; and 3 increased mortality. Sum value indicates the overall effect of climate change to a species.

Family and Species	Common name	Sea level rise	Ocean and air warming	Melting sea ice	Sum out of nine	References
Odobenidae						
Odobenus rosmarus	Walrus	1	1	2	4	(Tynan and DeMaster; 1997, MacCracken, 2012)
Otariidae						
Arctocephalus australis	South American fur seal	1	1	0	2	(Campagna, 2008a)
Arctocephalus forsteri	New Zealand fur seal	1	1	0	2	(Goldsworthy and Gales, 2008a)
Arctocephalus galapagoensis	Galápagos fur seal	2	2	0	4	(Würsig *et al.*, 2002. reviewed in Learmonth *et al.*, 2006)
Arctocephalus gazella	Antarctic fur seal	1	2	1	4	(Forcada *et al.*, 2005; Chapter Four)
Arctocephalus philippii	Juan Fernández fur seal	1	2	0	3	(Aurioles and Trillmich, 2008a)
Arctocephalus pusillus	Afro-Australian fur seal	1	1	1	3	(Hofmeyr and Gales, 2008; Schumann *et al.*, 2013)
Arctocephalus townsendi	Guadalupe fur seal	1	1	0	2	(Aurioles and Trillmich, 2008b)
Arctocephalus tropicalis	Subantarctic fur seal	1	2	0	3	(Hofmeyr and Kovacs, 2008; Oosthuizen *et al.*, 2016; Chapter Four)
Callorhinus ursinus	Northern fur seal	1	1	1	3	(Gelatt and Lowry, 2012)
Eumetopias jubatus	Steller sea lion	1	2	1	4	(National Marine Fisheries Service, 2008; Hastings *et al.*, 2011)
Neophoca cinerea	Australian sea lion	1	1	0	2	(Goldsworthy and Gales, 2008b; Schumann *et al.*, 2013)
Otaria flavescens	South American sea lion	1	1	0	2	(Campagna, 2008b)
Phocarctos hookeri	New Zealand sea lion	1	2	0	3	(Aurioles and Trillmich, 2008c; Robertson and Chilvers, 2015)
Zalophus californianus	California sea lion	1	2	0	4	(Aurioles-Gamboa *et al.*, 2003)
Zalophus wollebaeki	Galápagos sea lion	2	2	0	4	(Mueller *et al.*, 2011)
Phocidae						
Cystophora cristata	Hooded seal	1	1	3	5	(Johnston *et al.*, 2005; Laidre *et al.*, 2008)

Erignathus barbatus	Bearded seal	1	1	2	4	(Laidre *et al.*, 2008)
Halichoerus grypus	Grey seal	1	1	2	4	(Jussi *et al.*, 2008)
Histriophoca fasciata	Ribbon seal	1	1	2	4	(Burkanov and Lowry, 2008)
Hydrurga leptonyx	Leopard seal	1	2	3	6	(Southwell, 2008a)
Leptonychotes weddellii	Weddell seal	1	1	2	4	(Learmonth *et al.*, 2006; Proffitt *et al.*, 2007)
Lobodon carcinophagus	Crabeater seal	1	1	2	4	(Southwell, 2008b)
Mirounga angustirostris	Northern elephant seal	2	2	0	3	(McIntyre *et al.*, 2011; Funayama *et al.*, 2013)
Mirounga leonina	Southern elephant seal	1	2	2	5	(McIntyre *et al.*, 2011; Clausius *et al.*, 2017)
Monachus monachus	Mediterranean monk seal	2	1	0	4	(Harwood, 2001; di Sciara, 2016)
Monachus schauinslandi	Hawaiian monk seal	2	2	0	4	(Antonelis *et al.*, 2003; Baker *et al.*, 2006)
Ommatophoca rossi	Ross seal	1	1	2	4	(Southwell, 2008c)
Pagophilus groenlandica	Harp seal	1	1	3	5	(Johnston *et al.*, 2012)
Phoca largha	Spotted seal	1	2	3	6	(Tynan and DeMaster, 1997; Moore and Huntington, 2008)
Phoca vitulina	Common seal	1	1	2	4	(Thompson and Härkönen, 2008)
Pusa caspica	Caspian seal	1	2	3	6	(Harkonen *et al.*, 2008)
Pusa hispida	Ringed seal	2	1	3	6	(Ferguson *et al.*, 2005)
Pusa sibirica	Baikal seal	2	1	1	4	(Burkanov, 2008)

Intrinsic factors affecting population dynamics

Density-dependant regulation

One of the primary intrinsic factors limiting the population growth rates of *A. tropicalis* and *A. gazella* populations is density-dependant regulation (Table 2 and Table 3). Many *A. tropicalis* and *A. gazella* populations have recovered substantially from historical exploitation, leading to stable populations, and density-dependant limitation can now be observed in several well-established *A. tropicalis* and *A. gazella* populations. For example, during the last decade, the population growth rates of *A. tropicalis* at Marion Island and *A. gazella* at South Georgia have had a decrease in pup production through a reduction in female fecundity, caused by density-dependant limitation in prey resources, termed a population 'overshoot' (McMahon *et al.*, 2005; Wege *et al.*, 2016,). It may be expected that the above-mentioned *A. tropicalis* and *A. gazella* populations will stabilise within the coming years as the predator-prey relationship reaches an equilibrium. Although, the effects of increasing environmental variation may result in some *A. tropicalis* and *A. gazella* populations never reaching an equilibrium (Morley *et al.*, 2019).

Hybridisation

Although thought to be a rare phenomenon, hybridisation rates are now observed frequently and admixture rates are thought to be increasing, due to anthropogenic disturbances to natural ecosystems (Rhymer and Simberloff, 1996). Within the marine environment, otariids easily hybridise, due to their high density, polygynous and sympatric breeding colonies. With increased anthropogenic disturbances otariid seals hybrid zones may be expected to increase over the coming decades, as climate change causes an overlap of species breeding areas through a geographical shift in species ranges (Shurtliff, 2013).

There are a diverse array of studies on the effects of hybridisation (*e.g.* Barton, 2001; Arnold and Martin, 2010; Abbott *et al.*, 2013). However, many of these studies are in a laboratory setting, and only a few hybridisation studies combine long-term ecological analyses with the genomic information necessary to infer accurate estimates of hybrid fitness in a natural ecosystem. The Macquarie Island fur seal monitoring program

provided a unique opportunity to combine long-term ecological demographic data of hybrids with genomic information, allowing the survival probabilities of hybrids in the wild to be analysed.

In Chapter Three *A. tropicalis*, *A. gazella,* and New Zealand fur seals (*Arctocephalus forsteri*) hybrids at Macquarie Island had similar survival rates to pure species, with hybrid survival rates more closely reflecting the survival rates of *A. gazella* than *A. tropicalis*. These results expand the literature of hybrid fitness and provide the first survival estimates for fur seal hybrids. However, survival rates of hybrids and pure species can differ in other species (Neubauer *et al.*, 2014). Perhaps the comparable survival rates of Macquarie Islands *A. tropicalis*, *A. gazella* and hybrids is a consequence of severe backcrossing of the species since the recolonisation of Macquarie Island. This may have resulted in the Macquarie Island fur seals having a high genetic admixture which may contribute to having advantageous physiological or behavioural traits for survival in all three genotypes (Abbott *et al.*, 2013). Demographic studies within hybrid zones should therefore incorporate hybrid fitness (*i.e.* reproductive success and population growth) into demographic modelling as the Macquarie Island hybrid research may not be comparable to other hybrid zones. Even though hybridisation may only account for small differences in hybrid fitness, as small differences in survival rates between hybrids and pure species can translate to moderate or large differences in population trends over time, hybridisation should be accounted for in population modelling.

Interplay between intrinsic and extrinsic determinants of survival

Understanding the complex interplay of intrinsic and extrinsic factors which influence a population's growth over time is crucial for the development of population viability analysis, and the development of a management and conservation plan, if necessary (Little *et al.*, 2007). A review of the intrinsic and extrinsic factors which influence the survival responses and population growth rates of *A. tropicalis* and *A. gazella* at Macquarie Island, found a complex interplay of intrinsic and extrinsic factors (Table 2 and Table 3) that were important in determining the species' population dynamics.

While it is becoming increasingly apparent that climate change is the principal cause of many species population trajectories (*e.g.* Butchart *et al.*, 2010; Hoffmann and Sgro,

2011; Younger *et al.*, 2016; Clausius *et al.*, 2017). If intrinsic factors, such as life history traits, age and sex, are not taken into account when modelling population dynamics, predictions from extrinsic factors, such as environmental variation are likely to be imprecise.

Table 2. Population trends, primary factors limiting population growth and impending or secondary factors limiting population growth of *Arctocephalus tropicalis* populations. A dash (-) denotes no data to establish primary factors limiting population growth.

Population	Location	Global population (%)	Population trend	Primary factor limiting population growth	Impending or secondary factors limiting population growth	Reference
Gough Island	-	63.0	Stable	Density dependence	Climate change, fisheries interactions, disease	(Bester *et al.*, 2006; Hofmeyr, 2015)
Prince Edwards	Prince Edward Is	12.2	Increase	Density dependence	Climate change, fisheries interactions, disease	(Bester *et al.*, 2009; Hofmeyr, 2015)
	Marion Is	12.8	Decreasing	Density dependence	Climate change, fisheries interactions, entanglement, disease	(Hofmeyr and Bester, 2002; Wege *et al.*, 2016)
Amsterdam Island	-	11.0	Stable*	Density dependence	Climate change, fisheries interactions, disease	(Guinet *et al.*, 1994; Hofmeyr, 2015)
Îles Crozet	-	> 1.0	Increasing*	-	Climate change, fisheries interactions, disease	(SCAR-GSS, 2000; Hofmeyr, 2015)
St Paul Island	-	> 0.5	Increasing *	-	Climate change, fisheries interactions, disease	(SCAR-GSS, 2000; Hofmeyr, 2015)
Macquarie Island	-	> 0.5	Increasing	Predation from *Phocarctos hookeri*	Climate change, fisheries interactions, pollution, hybridisation	(Chapter Threee, Department of the Environment, 2016)
Heard Island	-	> 0.1	Stable	Density dependence	Climate change, fisheries interactions, pollution	(Department of the Environment, 2016)

* No current data available on population trends

Table 3. Population trends, primary factors limiting population growth and impending or secondary factors limiting population growth of *Arctocephalus gazella* populations. A dash (-) denotes no data to establish primary factors limiting population growth.

Population	Location	Global population (%)	Population trend	Primary factor limiting population growth	Impending or secondary factors limiting population growth	Reference
South Georgia	South Georgia Is	95.0	Declining	Climate mitigated changes in prey	Fisheries interactions disease, tourism	(Forcada and Hoffman, 2014; Hofmeyr, 2016)
	Bird Island Is	> 0.1	Increasing*	-	Climate change, fisheries interactions, entanglement	(Boyd *et al.*, 1995; Hofmeyr, 2016)
	South Sandwich Is	> 0.1	Stable*	-	Climate change, fisheries interactions, entanglement	(SCAR-GSS, 2000; Hofmeyr, 2016)
Nyrøysa	-	1.0	Declining	Density dependence	Climate change, fisheries interactions, entanglement	(Hofmeyr *et al.*, 2006a)
South Shetland Island	Cape Shirreff Is	> 0.5	Increasing	Predation from *Hydrurga leptonyx*	Climate change, fisheries interactions	(Hucke-Gaete *et al.*, 2004)
	Elephant Is	> 0.1	Increasing	Predation from *Hydrurga leptonyx*	Climate change, fisheries interactions	(Hucke-Gaete *et al.*, 2004)
Prince Edwards	Prince Edward Is	> 0.1	Increasing	-	Predation from *Orcinus orca,* entanglement	(Reisinger *et al.*, 2011)
	Marion Is	> 0.1	Increasing	-	Predation from *Orcinus orca,* entanglement	(Reisinger *et al.*, 2011)
Macquarie Island	-	> 0.1	Increasing	Predation from *Phocarctos hookeri*	Climate change, fisheries interactions, pollution, hybridisation	(Chapter Three, Department of the Environment, 2016)
Heard Island	-	> 0.1	Increasing	Climate change	Fisheries interactions, pollution	(Department of the Environment, 2016)
Seal Island	North Annex colony	> 0.1	Increasing*	-	Climate change, fisheries interactions	(SCAR-GSS, 2000; Hofmeyr, 2016)
	North Cove colony	> 0.1	Decreasing*	Predation from *Hydrurga leptonyx*	Climate change, fisheries interactions	(Boveng *et al.*, 1998)
Îles Crozet (Île de Possession)	-	> 0.1	Increasing*	-	Climate change, fisheries interactions	(SCAR-GSS, 2000; Hofmeyr, 2016)

* No current data available on population trends

Population management

Previous conservation and management strategies for the Macquarie Island fur seal population were concerned with the population growth of the threatened *A. tropicalis* (Environment Australia, 2004). Potential threats to the *A. tropicalis* population were identified as legal and illegal fishing, marine pollution, disease outbreaks, and disturbance from tourism and research. Climate, oceanographic change and predation were also identified as likely threats to the species (Department of Environment and Heritage, 2004; Environment Australia, 2004; Department of the Environment, 2016).

In the management of populations, modern emphasis is on SMART objectives (Specific, Measurable, Achievable, Results-oriented and Time-fixed objectives). In the management of small populations, which are vulnerable to stochastic factors, it is important to focus on manageable objectives which can be achieved in a short timeframe. As such, pup predation by New Zealand sea lions (*Phocarctos hookeri*) should be a key objective of the Macquarie Island population, as predation is considered a more tangible and manageable issue than environmental variation. Therefore, to facilitate increases in population growth rates of *A. tropicalis* the presence of *P. hookeri* at Macquarie Island should be managed. However, as *P. hookeri* are also an endangered species (Chilvers, 2015), this requires careful consideration. Removal of *P. hookeri* does not have to be lethal, the one or two sea lions which predate on pups could be encouraged to leave the breeding beaches by controlled harassment. Non-lethal rubber bullets and bean bag shells which are used to deter wolves and bears from livestock and human settlements, or acoustic harassment devices deployed at salmon sites to deter birds and seals could be employed at Macquarie Island (Shrivik, 2004; Fjalling *et al.*, 2006; Engeman *et al.*, 2009). To reduce the labour intensity of constantly patrolling the beaches to monitor *P. hookeri*'s presence, webcams could allow for remote monitoring of the beaches.

Although fisheries are a major threat for many pinniped species, the low numbers of seal entanglements in fishing gear at Macquarie Island (four in 2011/12; Alderman per comm., 2016) indicates the current state-level management scheme (protection for terrestrial breeding colonies, waters adjacent to breeding colonies) is effective for *A. tropicalis* and *A. gazella*. However, there are no data to establish *A. gazella* interactions with fisheries

outside of the breeding season and during winter migration, therefore this should be an area of future research.

Finally, while current populations are thriving, changing oceanographic conditions and extreme events, may be a future threat to the growth and recovery of *A. tropicalis* and *A. gazella* populations, especially due to their low numbers (Gerber and Hilborn, 2001). Therefore, long-term annual monitoring of the Macquarie Island population should resume until the population numbers of *A. tropicalis* are at the very least over 500. This estimate is based on the 50/500 rule Franklin (1980). Fifty individuals are needed to prevent immediate population extinction from inbreeding and demographic stochasticity, and 500 individuals is the minimum viable population size to reduce the likelihood of local extinction due to environmental and demographic stochasticity (Gerber and Hilborn, 2001). However, current research dictates 500 individuals is too low of a number to ensure population survival, and a population size of at least 5000 individuals is needed for a population to persist in the face of environmental variation (Traill *et al.*, 2009). Therefore, following best practice for conservation, long-term annual monitoring of the Macquarie Island population should resume until the population numbers of *A. tropicalis* are over 5000. Furthermore, six years of additional resight data in conjunction with the existing 26-years of resight data will provide information on population trends over three generations for *A. tropicalis* and *A. gazella,* which is the minimum amount of data needed to establish a population trend.

Future directions

Several important questions remain to be answered; in particular, the effects of hybridisation on fecundity rates, and the full extent of hybridisation on Macquarie Island as well as the winter foraging distribution of *A. gazella*.

Although, the reproductive success of male hybrids has been studied (Lancaster *et al.*, 2007a), uncertainty around the effects of hybridisation on the fecundity of female *A. gazella* and *A. tropicalis* at Macquarie Island remains (Chapter Three). Survival and reproductive success rates are fundamental to understanding population dynamics (Eberhardt and Siniff, 1977).

Furthermore, to understand the full extent of hybridisation, future studies should utilise the skin biopsies collected from 2000-2001 and 2005–2011, and employ next-generation DNA sequencing technologies, such as Restriction site Associated DNA Sequencing, which is effective in detecting backcrosses beyond the third generation (Twyford and Ennos, 2012). Detection of backcrosses will enable survival and fecundity rate estimates of different classes of hybrids, thus furthering our understanding of the role of hybridisation in evolution and speciation.

Differences in survival *A. gazella* and *A. tropicalis* in relation to environmental variables is likely to be due to their differing life histories, in particular differences in non-breeding winter foraging strategies. The availability of information on winter foraging movements is limited to non-Macquarie Island populations (Arthur *et al.*, 2015; Kirkman *et al.*, 2016). Information on winter foraging behaviour could be obtained if breeding *A. gazella* females at Macquarie Island are captured during the latter part of lactation (February–March) and fitted with global location sensing (GLS) loggers, which can track foraging movements over an eight to nine-month period. The winter-foraging migration behaviour of *A. gazella* should help explain why *A. gazella* have a higher survival rate than *A. tropicalis* during periods of high sea level pressure and higher sea surface temperature could be identified (Chapter Four).

In summary, the Macquarie Island fur seal program provided important long-term data on population recovery, survival and ecological performance indicators for key Southern Ocean meso-predators. Maintaining such monitoring programs is vital to better understanding the demographic responses of meso-predators to environmental changes in the Southern Ocean.

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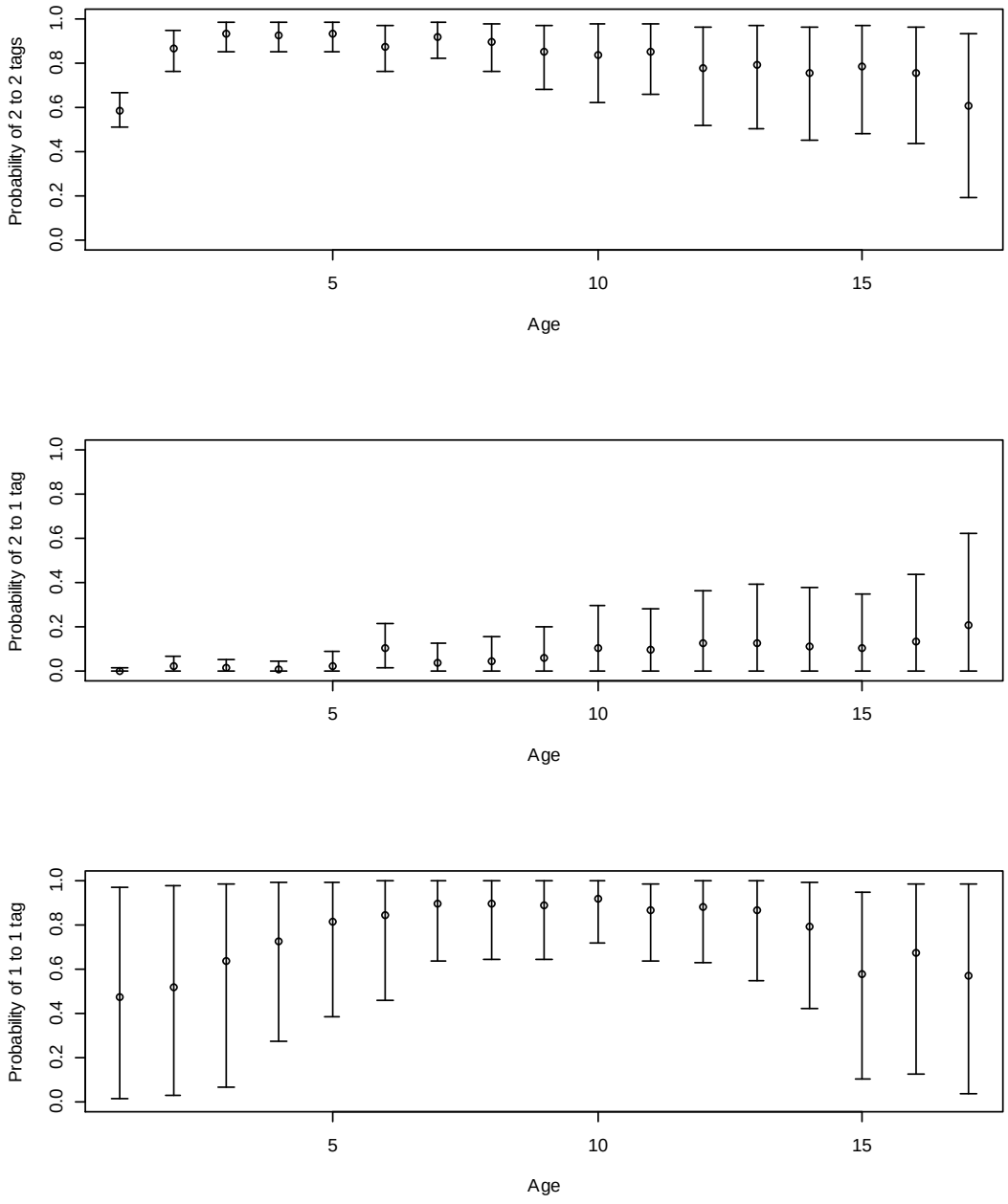
Appendix A. Markovian matrix to describe the transition between states in the multi-event multi-state model for tag loss in fur seals of all age groups. Φ (survival), d2 detecting two tags, d1 detecting one tag, $\psi_{2:2}$ two tags to two tags, $\psi_{2:1}$ two tags to one tag, *d*R (probability of detecting an RFID tag given one or two tags), dR^0 (probability of detecting an RFID tag given zero tags).

	State at t+1												
State at t	1	2	3	4	5	6	7	8	9	10	11	12	13
1	Φ $\psi_{2:2}$ d2 dR	Φ $\psi_{2:2}$ d2 (1-dR)	Φ $\psi_{2:2}$ (1-d2) (1-dR)	Φ $\psi_{2:1}$ d1 dR	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	Φ $\psi_{2:2}$ 2 d2 (1-dR)	Φ $\psi_{2:2}$ (1-d2) (1-dR)	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	Φ $\psi_{2:0}$ dR^0	Φ $\psi_{2:0}$ (1-dR^0)	1-Φ
2	Φ $\psi_{2:2}$ d2 dR	Φ $\psi_{2:2}$ d2 (1-dR)	Φ $\psi_{2:2}$ (1-d2) (1-dR)	Φ $\psi_{2:1}$ d1 dR	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	Φ $\psi_{2:2}$ d2 (1-dR)	Φ $\psi_{2:2}$ (1-d2) (1-dR)	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	Φ $\psi_{2:0}$ dR^0	Φ $\psi_{2:0}$ (1-dR^0)	1-Φ
3	Φ $\psi_{2:2}$ d2 dR	Φ $\psi_{2:2}$ d2 (1-dR)	Φ $\psi_{2:2}$ (1-d2) (1-dR)	Φ $\psi_{2:1}$ d1 dR	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	Φ $\psi_{2:2}$ d2 (1-dR)	Φ $\psi_{2:2}$ (1-d2) (1-dR)	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	Φ $\psi_{2:0}$ dR^0	Φ $\psi_{2:0}$ (1-dR^0)	1-Φ
4	0	0	0	Φ $\psi_{1:1}$ d1 dR	Φ $\psi_{1:1}$ d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	0	0	Φ $\psi_{1:1}$ d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	Φ $\psi_{1:0}$ dR^0	Φ $\psi_{1:0}$ (1-dR^0)	1-Φ
5	0	0	0	Φ $\psi_{1:1}$ d1 dR	Φ $\psi_{1:1}$ d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	0	0	Φ ψ1:1 d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	Φ $\psi_{1:0}$ dR^0	Φ $\psi_{1:0}$ (1-dR^0)	1-Φ
6	0	0	0	Φ $\psi_{1:1}$1 d1 dR	Φ $\psi_{1:1}$ d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	0	0	Φ $\psi_{1:1}$ d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	Φ $\psi_{1:0}$ dR^0	Φ $\psi_{1:0}$ (1-dR^0)	1-Φ
7	0	0	0	0	0	0	0	0	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	0	0	1-Φ
8	0	0	0	0	0	0	0	0	Φ $\psi_{2:1}$ d1 (1-dR)	Φ $\psi_{2:1}$ (1-d1) (1-dR)	0	0	1-Φ
9	0	0	0	0	0	0	0	0	Φ $\psi_{1:1}$ d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	0	0	1-Φ
10	0	0	0	0	0	0	0	0	Φ $\psi_{1:1}$ d1 (1-dR)	Φ $\psi_{1:1}$ (1-d1) (1-dR)	0	0	1-Φ
11	0	0	0	0	0	0	0	0	0	0	Φ dR^0	Φ (1- dR^0)	1-Φ
12	0	0	0	0	0	0	0	0	0	0	Φ dR^0	Φ (1-dR^0)	1-Φ
Dead	0	0	0	0	0	0	0	0	0	0	0	0	1



Appendix B. Tag loss probabilities of female *Arctocephalus gazella* as a function of age showing wide 95% credible intervals due to reduced sample size.

Appendix C. Posterior distribution of tag loss transition probabilities as a function of age classes, sex and species. Sample size for tags transitions from one tag to one tag or one tag to zero tags was limited so cohorts were grouped as all ages. 95% posterior intervals are in parentheses.

		Arctocephalus tropicalis		*Arctocephalus gazella*	
Age	**Tag transition**	**Female**	**Male**	**Female**	**Male**
Pups	2 to 2	0.49 (0.37, 0.61)	0.56 (0.42, 0.69)	0.43 (0.36, 0.49)	0.63 (0.56, 0.70)
	2 to 1	0.08 (0.03, 0.15)	0.13 (0.06, 0.24)	0.10 (0.06, 0.14)	0.01 (0.06, 0.14)
	2 to 0	0.44 (0.31, 0.56)	0.31 (0.18, 0.46)	0.48 (0.41, 0.54)	0.27 (0.21, 0.35)
Juveniles	2 to 2	0.85 (0.70, 0.96)	0.86 (0.71, 0.96)	0.88 (0.81, 0.94)	0.95 (0.90, 0.98)
	2 to 1	0.07 (0.01, 0.17)	0.07 (0.01, 0.18)	0.04 (0.01, 0.09)	0.02 (0.00, 0.05)
	2 to 0	0.08 (0.01, 0.22)	0.07 (0.01, 0.20)	0.08 (0.03, 0.15)	0.03 (0.01, 0.08)
Adults	2 to 2	0.89 (0.85, 0.93)	0.93 (0.89, 0.97)	0.90 (0.88, 0.91)	0.94 (0.92, 0.96)
	2 to 1	0.07 (0.04, 0.10)	0.04 (0.01, 0.07)	0.04 (0.03, 0.06)	0.04 (0.02, 0.05)
	2 to 0	0.04 (0.02, 0.08)	0.03 (0.01, 0.06)	0.06 (0.05, 0.08)	0.03 (0.01, 0.04)
All ages	1 to 1	0.88 (0.80, 0.95)	0.88 (0.74, 0.97)	0.94 (0.91, 0.97)	0.92 (0.86, 0.96)
	1 to 0	0.12 (0.05, 0.20)	0.12 (0.03, 0.26)	0.06 (0.03, 0.09)	0.08 (0.04, 0.14)

Appendix D. Demographic overview of *Arctocephalus gazella* at Macquarie Island from 1986–2011. Age and sex structure for all animals resighted each breeding season. Percentages in parentheses. Resights during 2004 could not be conducted throughout the entire breeding season, so resight numbers are lower.

Year	Pups (0 – 1 yrs)	Juveniles (2 – 3 yrs)	Adults (≥ 4 yrs)	Male	Female	Unknown sex	TOTAL
1986	21 (91.3)	1 (4.3)	1 (4.3)	8 (34.8)	15 (65.2)	0 (0.0)	23
1987	19 (100)	0 (0.0)	0 (0.0)	11 (57.9)	8 (42.1)	0 (0.0)	19
1988	25 (86.2)	4 (13.8)	0 (0.0)	14 (48.3)	15 (51.7)	0 (0.0)	29
1989	15 (48.4)	7 (22.6)	9 (29.0)	14 (45.2)	17 (54.8)	0 (0.0)	31
1990	36 (43.9)	11 (13.4)	35 (42.7)	28 (34.1)	54 (65.9)	0 (0.0)	82
1991	39 (56.5)	0 (0.0)	30 (43.5)	23 (33.3)	46 (66.7)	0 (0.0)	69
1992	58 (59.2)	15 (15.3)	25 (25.5)	50 (51.0)	48 (49.0)	0 (0.0)	98
1993	69 (65.7)	14 (13.3)	22 (21.0)	46 (43.8)	59 (56.2)	0 (0.0)	105
1994	77 (60.6)	22 (17.3)	28 (22.0)	59 (46.5)	68 (53.5)	0 (0.0)	127
1995	82 (43.2)	35 (18.4)	73 (38.4)	81 (42.6)	108 (56.8)	1 (0.5)	190
1996	98 (45.6)	5 (2.3)	112 (52.1)	71 (33.0)	138 (64.2)	6 (2.8)	215
1997	96 (35.4)	44 (16.2)	131 (48.3)	114 (42.1)	155 (57.2)	2 (0.7)	271
1998	85 (50.3)	11 (6.5)	73 (43.2)	65 (38.5)	102 (60.4)	2 (1.2)	169
1999	72 (29.0)	34 (13.7)	142 (57.3)	101 (40.7)	145 (58.5)	2 (0.8)	248
2000	115 (41.1)	35 (12.5)	130 (46.4)	99 (35.3)	177 (63.3)	4 (1.4)	280
2001	113 (40.4)	36 (12.9)	131 (46.8)	122 (43.6)	152 (54.3)	6 (2.1)	280
2002	70 (43.2)	7 (4.3)	85 (52.5)	39 (24.1)	121 (74.7)	2 (1.2)	162
2003	113 (42.8)	30 (11.4)	121 (45.8)	83 (31.5)	177 (67.0)	4 (1.5)	264
2004	58 (98.3)	0 (0.0)	1 (1.7)	29 (49.2)	30 (50.8)	0 (0.0)	59
2005	142 (51.4)	11 (4.0)	123 (44.6)	88 (31.9)	179 (64.9)	9 (3.3)	276
2006	154 (45.2)	44 (12.9)	143 (41.9)	125 (36.9)	211 (62.2)	3 (0.9)	341
2007	148 (49.3)	29 (9.7)	123 (41.0)	121 (40.3)	178 (59.3)	1 (0.3)	300
2008	138 (38.4)	45 (12.5)	176 (49.0)	134 (37.3)	223 (62.2)	2 (0.5)	359
2009	126 (37.8)	45 (13.5)	162 (48.6)	120 (36.1)	210 (63.3)	3 (0.6)	333
2010	143 (28.8)	92 (18.5)	262 (52.7)	181 (36.4)	314 (63.2)	2 (0.4)	497
2011	184 (30.0)	105 (17.1)	324 (52.9)	245 (39.0)	366 (59.8)	2 (0.3)	613

Appendix E. Demographic overview of *Arctocephalus tropicalis* at Macquarie Island from 1986–2011. Age and sex structure for all animals resighted each breeding season. Percentages in parentheses. Resights during 2004 could not be conducted throughout the entire breeding season, so resight numbers are lower.

Year	Pups (0 – 1 yrs)	Juveniles (2 – 4 yrs)	Adults (≥ 5 yrs)	Male	Female	Unknown sex	TOTAL
1986	7 (100)	0 (0.0)	0 (0.0)	1 (14.3)	6 (85.7)	0 (0.0)	7
1987	9 (81.8)	1 (9.1)	1 (9.1)	5 (45.5)	6 (54.5)	0 (0.0)	11
1988	12 (80.0)	3 (20.0)	0 (0.0)	7 (46.7)	8 (53.3)	0 (0.0)	15
1989	12 (66.7)	6 (33.3)	0 (0.0)	8 (44.4)	10 (55.6)	0 (0.0)	18
1990	15 (50.0)	8 (26.7)	7 (23.3)	12 (40.0)	18 (60.0)	0 (0.0)	30
1991	22 (71.0)	1 (3.2)	8 (25.8)	10 (32.3)	21 (67.7)	0 (0.0)	31
1992	19 (52.8)	10 (27.8)	7 (19.4)	13 (36.1)	23 (63.9)	0 (0.0)	36
1993	20 (48.8)	9 (23.6)	9 (23.6)	15 (39.5)	23 (60.5)	0 (0.0)	38
1994	17 (47.2)	8 (22.2)	11 (30.6)	12 (33.3)	24 (66.7)	0 (0.0)	36
1995	23 (29.1)	22 (27.8)	34 (43.0)	28 (35.4)	51 (64.6)	0 (0.0)	79
1996	21 (29.2)	3 (4.2)	48 (66.7)	21 (29.2)	51 (70.8)	0 (0.0)	72
1997	28 (27.2)	22 (21.4)	53 (51.5)	32 (31.1)	67 (65.0)	4 (3.9)	103
1998	30 (39.0)	16 (20.8)	31 (40.3)	37 (48.1)	39 (50.6)	1 (1.3)	77
1999	9 (12.0)	25 (33.3)	41 (54.7)	30 (40.0)	45 (60.0)	0 (0.0)	75
2000	30 (37)	19 (23.5)	32 (39.5)	31 (38.3)	49 (60.5)	1 (1.2)	81
2001	32 (37.2)	25 (29.1)	29 (33.7)	27 (31.4)	57 (66.3)	2 (2.3)	86
2002	36 (48.6)	21 (28.4)	17 (23.0)	39 (52.7)	35 (47.3)	0 (0.0)	74
2003	40 (59.7)	7 (10.4)	20 (29.9)	27 (40.3)	39 (58.2)	1 (1.5)	67
2004	14 (100.0)	0 (0.0)	0 (0.0)	9 (64.3)	5 (35.7)	0 (0.0)	14
2005	35 (64.8)	2 (3.7)	17 (31.5)	16 (29.6)	35 (64.8)	3 (5.6)	54
2006	37 (51.4)	10 (13.9)	25 (34.7)	35 (48.6)	37 (51.4)	0 (0.0)	72
2007	42 (60.9)	2 (2.9)	25 (36.2)	26 (37.7)	43 (62.3)	0 (0.0)	69
2008	48 (50.5)	9 (9.5)	38 (40.0)	43 (45.3)	52 (54.7)	0 (0.0)	95
2009	48 (46.6)	8 (7.8)	47 (45.6)	51 (49.5)	52 (50.5)	0 (0.0)	103
2010	51 (31.9)	46 (28.8)	63 (39.4)	80 (50.0)	80 (50.0)	0 (0.0)	160
2011	47 (24.2)	56 (28.9)	91 (46.9)	83 (42.8)	111 (57.2)	0 (0.0)	194

Appendix F. Supporting table for figure 1a in Chapter Three. Number of all animals (*Arctocephalus gazella*, *Arctocephalus tropicalis*, *Arctocephalus forsteri*, hybrid fur seals and fur seals whose species could not be identified) resighted at Macquarie Island during each breeding season between 1986–2011. Percentages in parentheses. Resights during 2004 could not be conducted throughout the entire breeding season, so resight numbers are lower. Species identification is based on phenotypic assessment; therefore, the number of hybrids identified may be misidentified by up to 75%.

Year	*A. gazella*	*A. tropicalis*	*A. forsteri*	Hybrid	Unidentified	Total
1986	23 (36.5)	7 (11.1)	2 (3.2)	2 (3.2)	29 (46)	63
1987	19 (42.2)	11 (24.4)	1 (2.2)	1 (2.2)	13 (28.9)	45
1988	29 (45.3)	15 (23.4)	1 (1.6)	1 (1.7)	18 (28.1)	64
1989	31 (32.3)	18 (18.8)	3 (3.1)	14 (14.6)	30 (31.3)	96
1990	82 (56.9)	30 (20.8)	3 (2.1)	12 (8.3)	17 (11.8)	144
1991	69 (52.3)	31 (23.5)	2 (1.5)	19 (14.4)	11 (8.3)	132
1992	98 (47.8)	36 (17.6)	3 (1.5)	14 (6.8)	54 (26.3)	205
1993	105 (48.4)	38 (17.5)	3 (1.4)	11 (5.1)	60 (27.6)	217
1994	127 (51.8)	36 (14.7)	2 (0.8)	18 (7.3)	62 (25.3)	245
1995	215 (59.4)	72 (19.9)	3 (0.8)	17 (4.7)	55 (15.2)	362
1996	190 (53.5)	79 (22.3)	3 (0.8)	22 (6.2)	61 (17.2)	355
1997	271 (58.9)	103 (22.4)	3 (0.7)	30 (6.5)	53 (11.5)	460
1998	169 (54.0)	77 (24.6)	3 (1.0)	26 (8.3)	38 (12.1)	313
1999	248 (54.6)	75 (16.5)	2 (0.4)	34 (7.5)	95 (20.9)	454
2000	280 (68.0)	81 (19.7)	1 (0.2)	20 (4.9)	30 (7.3)	412
2001	280 (67.3)	86 (20.7)	2 (0.5)	22 (5.3)	26 (6.3)	416
2002	162 (54.2)	74 (24.7)	0 (0.0)	43 (14.4)	20 (6.7)	299
2003	264 (72.9)	67 (18.5)	0 (0.0)	14 (3.9)	17 (4.7)	362
2004	59 (77.6)	14 (18.4)	1 (1.3)	1 (1.3)	1 (1.3)	76
2005	276 (74.6)	54 (14.6)	0 (0.0)	24 (6.5)	16 (4.3)	370
2006	341 (75.4)	72 (15.9)	0 (0.0)	17 (3.8)	22 (4.9)	452
2007	300 (75.8)	69 (17.4)	0 (0.0)	18 (4.5)	9 (2.3)	396
2008	359 (71.7)	95 (19.0)	0 (0.0)	34 (6.8)	13 (2.6)	501
2009	333 (65.3)	103 (20.2)	0 (0.0)	67 (13.1)	7 (1.4)	510
2010	497 (66.1)	160 (21.3)	0 (0.0)	88 (11.7)	7 (0.9)	752
2011	613 (69.4)	194 (20.1)	2 (0.2)	64 (7.2)	10 (1.1)	883

Appendix G. Punnett square for *Arctocephalus gazella* (G), *Arctocephalus tropicalis* (T) and *Arctocephalus forsteri* (F) over three generations, showing the genotype of three generations of interspecies bredding.

Mother \ Father	G	T	F	GT	GF	TF	G-GT	G-GF	G-TF	T-GT	T-GF	T-TF	F-GT	F-GF	F-TF	GT-GT	GT-GF	GT-TF	GF-GF	GF-TF	TF-TF
G	GAZ	GT	GF	G-GT	G-GF	G-TF	G-G.GT	G-G.GF	G-G.TF	G-T.GT	G-T.GF	G-T.TF	G-F.GT	G-F.GF	G-F.TF	G-GT.GT	G-GT.GF	G-GT.TF	G-GF.GF	G-GF.TF	G-TF.TF
T	GT	TRO	TF	T-GT	T-GF	T-TF	T-G.GT	T-G.GF	T-G.TF	T-T.GT	T-T.GF	T-T.TF	T-F.GT	T-F.GF	T-F.TF	T-GT.GT	T-GT.GF	T-GT.TF	T-GF.GF	T-GF.TF	T-TF.TF
GT	GT-G	GT-T	GT-F	GT-GT	GT-GF	GT-TF	GT-G.GT	GT-G.GF	GT-G.TF	GT-T.GT	GT-T.GF	GT-T.TF	GT-F.GT	GT-F.GF	GT-F.TF	GT-GT.GT	GT-GT.GF	GT-GT.TF	GT-GF.GF	GT-GF.TF	GT-TF.TF
GF	GF-G	GF-T	GF-F	GF-GT	GF-GF	GF-TF	GF-G.GT	GF-G.GF	GF-G.TF	GF-T.GT	GF-T.GF	GF-T.TF	GF-F.GT	GF-F.GF	GF-F.TF	GF-GT.GT	GF-GT.GF	GF-GT.TF	GF-GF.GF	GF-GF.TF	GF-TF.TF
TF	TF-G	TF-T	TF-F	TF-GT	TF-GF	TF-TF	TF-G.GT	TF-G.GF	TF-G.TF	TF-T.GT	TF-T.GF	TF-T.TF	TF-F.GT	TF-F.GF	TF-F.TF	TF-GT.GT	TF-GT.GF	TF-GT.TF	TF-GF.GF	TF-GF.TF	TF-TF.TF
G-GT	G.GT-G	G.GT-T	G.GT-F	G.GT-GT	G.GT-GF	G.GT-TF	G.GT-G.GT	G.GT-G.GF	G.GT-G.TF	G.GT-T.GT	G.GT-T.GF	G.GT-T.TF	G.GT-F.GT	G.GT-F.GF	G.GT-F.TF	G.GT-GT.GT	G.GT-GT.GF	G.GT-GT.TF	G.GT-GF.GF	G.GT-GF.TF	G.GT-TF.TF
G-GF	G.GF-G	G.GF-T	G.GF-F	G.GF-GT	G.GF-GF	G.GF-TF	G.GF-G.GT	G.GF-G.GF	G.GF-G.TF	G.GF-T.GT	G.GF-T.GF	G.GF-T.TF	G.GF-F.GT	G.GF-F.GF	G.GF-F.TF	G.GF-GT.GT	G.GF-GT.GF	G.GF-GT.TF	G.GF-GF.GF	G.GF-GF.TF	G.GF-TF.TF
G-TF	G.TF-G	G.TF-T	G.TF-F	G.TF-GT	G.TF-GF	G.TF-TF	G.TF-G.GT	G.TF-G.GF	G.TF-G.TF	G.TF-T.GT	G.TF-T.GF	G.TF-T.TF	G.TF-F.GT	G.TF-F.GF	G.TF-F.TF	G.TF-GT.GT	G.TF-GT.GF	G.TF-GT.TF	G.TF-GF.GF	G.TF-GF.TF	G.TF-TF.TF
T-GT	T.GT-G	T.GT-T	T.GT-F	T.GT-GT	T.GT-GF	T.GT-TF	T.GT-G.GT	T.GT-G.GF	T.GT-G.TF	T.GT-T.GT	T.GT-T.GF	T.GT-T.TF	T.GT-F.GT	T.GT-F.GF	T.GT-F.TF	T.GT-GT.GT	T.GT-GT.GF	T.GT-GT.TF	T.GT-GF.GF	T.GT-GF.TF	T.GT-TF.TF
T-GF	T.GF-G	T.GF-T	T.GF-F	T.GF-GT	T.GF-GF	T.GF-TF	T.GF-G.GT	T.GF-G.GF	T.GF-G.TF	T.GF-T.GT	T.GF-T.GF	T.GF-T.TF	T.GF-F.GT	T.GF-F.GF	T.GF-F.TF	T.GF-GT.GT	T.GF-GT.GF	T.GF-GT.TF	T.GF-GF.GF	T.GF-GF.TF	T.GF-TF.TF
T-TF	T.TF-G	T.TF-T	T.TF-F	T.TF-GT	T.TF-GF	T.TF-TF	T.TF-G.GT	T.TF-G.GF	T.TF-G.TF	T.TF-T.GT	T.TF-T.GF	T.TF-T.TF	T.TF-F.GT	T.TF-F.GF	T.TF-F.TF	T.TF-GT.GT	T.TF-GT.GF	T.TF-GT.TF	T.TF-GF.GF	T.TF-GF.TF	T.TF-TF.TF
F-GT	F.GT-G	F.GT-T	F.GT-F	F.GT-GT	F.GT-GF	F.GT-TF	F.GT-G.GT	F.GT-G.GF	F.GT-G.TF	F.GT-T.GT	F.GT-T.GF	F.GT-T.TF	F.GT-F.GT	F.GT-F.GF	F.GT-F.TF	F.GT-GT.GT	F.GT-GT.GF	F.GT-GT.TF	F.GT-GF.GF	F.GT-GF.TF	F.GT-TF.TF
F-GF	F.GF-G	F.GF-T	F.GF-F	F.GF-GT	F.GF-GF	F.GF-TF	F.GF-G.GT	F.GF-G.GF	F.GF-G.TF	F.GF-T.GT	F.GF-T.GF	F.GF-T.TF	F.GF-F.GT	F.GF-F.GF	F.GF-F.TF	F.GF-GT.GT	F.GF-GT.GF	F.GF-GT.TF	F.GF-GF.GF	F.GF-GF.TF	F.GF-TF.TF
F-TF	F.TF-G	F.TF-T	F.TF-F	F.TF-GT	F.TF-GF	F.TF-TF	F.TF-G.GT	F.TF-G.GF	F.TF-G.TF	F.TF-T.GT	F.TF-T.GF	F.TF-T.TF	F.TF-F.GT	F.TF-F.GF	F.TF-F.TF	F.TF-GT.GT	F.TF-GT.GF	F.TF-GT.TF	F.TF-GF.GF	F.TF-GF.TF	F.TF-TF.TF
GT-GT	GT.GT-G	GT.GT-T	GT.GT-F	GT.GT-GT	GT.GT-GF	GT.GT-TF	GT.GT-G.GT	GT.GT-G.GF	GT.GT-G.TF	GT.GT-T.GT	GT.GT-T.GF	GT.GT-T.TF	GT.GT-F.GT	GT.GT-F.GF	GT.GT-F.TF	GT.GT-GT.GT	GT.GT-GT.GF	GT.GT-GT.TF	GT.GT-GF.GF	GT.GT-GF.TF	GT.GT-TF.TF
GT-GF	GT.GF-G	GT.GF-T	GT.GF-F	GT.GF-GT	GT.GF-GF	GT.GF-TF	GT.GF-G.GT	GT.GF-G.GF	GT.GF-G.TF	GT.GF-T.GT	GT.GF-T.GF	GT.GF-T.TF	GT.GF-F.GT	GT.GF-F.GF	GT.GF-F.TF	GT.GF-GT.GT	GT.GF-GT.GF	GT.GF-GT.TF	GT.GF-GF.GF	GT.GF-GF.TF	GT.GF-TF.TF
GT-TF	GT.TF-G	GT.TF-T	GT.TF-F	GT.TF-GT	GT.TF-GF	GT.TF-TF	GT.TF-G.GT	GT.TF-G.GF	GT.TF-G.TF	GT.TF-T.GT	GT.TF-T.GF	GT.TF-T.TF	GT.TF-F.GT	GT.TF-F.GF	GT.TF-F.TF	GT.TF-GT.GT	GT.TF-GT.GF	GT.TF-GT.TF	GT.TF-GF.GF	GT.TF-GF.TF	GT.TF-TF.TF
GF-GF	GF.GF-G	GF.GF-T	GF.GF-F	GF.GF-GT	GF.GF-GF	GF.GF-TF	GF.GF-G.GT	GF.GF-G.GF	GF.GF-G.TF	GF.GF-T.GT	GF.GF-T.GF	GF.GF-T.TF	GF.GF-F.GT	GF.GF-F.GF	GF.GF-F.TF	GF.GF-GT.GT	GF.GF-GT.GF	GF.GF-GT.TF	GF.GF-GF.GF	GF.GF-GF.TF	GF.GF-TF.TF
GF-TF	GF.TF-G	GF.TF-T	GF.TF-F	GF.TF-GT	GF.TF-GF	GF.TF-TF	GF.TF-G.GT	GF.TF-G.GF	GF.TF-G.TF	GF.TF-T.GT	GF.TF-T.GF	GF.TF-T.TF	GF.TF-F.GT	GF.TF-F.GF	GF.TF-F.TF	GF.TF-GT.GT	GF.TF-GT.GF	GF.TF-GT.TF	GF.TF-GF.GF	GF.TF-GF.TF	GF.TF-TF.TF
TF-TF	TF.TF-G	TF.TF-T	TF.TF-F	TF.TF-GT	TF.TF-GF	TF.TF-TF	TF.TF-G.GT	TF.TF-G.GF	TF.TF-G.TF	TF.TF-T.GT	TF.TF-T.GF	TF.TF-T.TF	TF.TF-F.GT	TF.TF-F.GF	TF.TF-F.TF	TF.TF-GT.GT	TF.TF-GT.GF	TF.TF-GT.TF	TF.TF-GF.GF	TF.TF-GF.TF	TF.TF-TF.TF

Appendix H. Summary of global and local metrological data available from Macquarie Island station (54°37° S, 158°51° E), and their effects on Southern Ocean predators.

Environmental variable	Year from which data is available	Environmental effect	Species response	References
GLOBAL				
Chlorophyll *a*	1995	The Southern Ocean is generally considered to have low concentrations of Chlorophyll *a*, which is limited by iron. Increased Chlorophyll *a* is linked with increased primary productivity.	On a small spatial scale, *Arctocephalus gazella* foraging activity was negatively related to surface chlorophyll levels. However, at a larger spatial scale foraging effort decreased in response to increased surface chlorophyll.	(Guinet *et al.*, 2001)
Currents	1991	Currents are associated with fronts and eddies. Increased current strength is associated with increased mixing layers, enhancing primary production. Surface currents are correlated with wind speed.	*Mirounga leonina* decreased foraging effort and foraging distance in response to stronger eddies and fronts.	(Dragon *et al.*, 2010)

Table continued …

El Niño–Southern Oscillation (ENSO)	1982	ENSO has three phases: El Niño: Ocean temperature is warmer than average sea surface SST. This is associated with a deeper thermocline and weakened westerly winds. La Niña: Ocean temperature is cooler than average sea surface SST. This is associated with the thermocline moving closer to the surface and stronger westerly winds. Neutral: Ocean temperatures are similar to average sea surface SST.	Warmer waters associated with negative ENSO, redistributes prey, increasing foraging effort and decreasing foraging success of adult *M. leonina*. This in turn reduced *M. leonina* pup weaning mass.	(Le Boeuf and Crocker, 2005; McMahon and Burton, 2005)
Sea Surface Height Anomaly (SSHA)	1992	SSHA is closely coupled with SST (Solanki *et al.*, 2015). It is the difference between the best estimate of the satellite-observed sea surface height and a mean sea surface. Warmer, less dense water column has a larger specific volume leading to an increase in surface height and pressure compared to the surrounding ocean.	Population responses are similar to SST responses.	

Table continued …

Southern Annular Mode (SAM)	1982	SAM has two phases: Positive: Westerly wind belt contracts towards Antarctica, and a low-pressure system develops over Antarctica, increases climate variability, upwelling of iron resulting in an increase in phytoplankton abundance in the Antarctic Zone. However, at the Subantarctic zone chlorophyll concentration decreases, due to deeper mixed layers decreasing light penetration into the water column. Negative: Westerly wind belt moves north towards Australia, and a high-pressure system develops over Antarctica, decreases climate variability, slowing upwelling lowering phytoplankton abundance in the Antarctic Zone. However, at the Subantarctic zone chlorophyll concentration increases, due to increased upwelling (Lovenduski and Gruber, 2005).	*Pygoscelis adeliae* population numbers in the Scotia Sea, declined in response to positive SAM.	(Forcada and Trathan, 2009)
Southern Oscillation Index (SOI)	1982	The Southern Oscillation is the atmospheric aspect of ENSO, ENSO is measured by the SOI and has two phases: Positive: Values above seven often indicate La Niña, and associated stronger trade winds, cold waters Negative: Values below seven often indicate El Niño, and weaker trade winds and warmer waters	*Mirounga leonina* first-year survival decreased in relation to negative SOI, which is related to female *M. leonina* ability to acquire resources.	(McMahon and Burton, 2005)

Table continued …

Sea Surface Temperature (SST)	1982	Colder waters have shallow thermoclines and are associated with increased primary production.	Lactating *Arctocephalus tropicalis* females at Amsterdam Island increased their foraging distance during periods of high SST.	(Georges *et al.*, 2000)
			Arctocephalus gazella pup production at South Georgia decreased in response to increased SST. This was linked to ENSO.	(Forcada *et al.*, 2005)
			Arctocephalus tropicalis at Gough and Marion Islands weaning mass increased in response to cooler waters.	(Oosthuizen *et al.*, 2016)
Wind speed	1982	Increased wind speed is associated with lower SST, increased mixing, more nutrients	*Eudyptes chrysocome* foraging mass gain increased in response to a moderate increase in wind speed.	(Dehnhard *et al.*, 2013)

Table continued …

LOCAL				
Rain	1948	Precipitation levels at Macquarie Island have increased by 9% in the summer, 20% in autumn, and 55% in winter (Adams, 2009).	None	
Sea level pressure	1948	Sea level pressure is related to the SOI (Kwok and Comiso, 2002). At Macquarie Island, there is a clear upward trend in the number of moderate changes crossing the island has occurred, with an increase from around 10 events per month to nearly 15 per month (Adams, 2009).	Population responses are similar to SOI responses.	
Temperature	1948	Changes in the air temperature	At higher temperatures more seals haul out, contributing to an increase in disease spread. *Arctocephalus pusillus* heat stress and mortality rates increased with warmer air conditions.	(Lavigne and Schmitz, 1990) (Devilliers and Roux, 1992)

Table continued …

Wind speed	1948	Increased wind speed is associated with lower SST, increased mixing, more nutrients	*Eudyptes chrysocome* foraging mass gain increased in response to a moderate increase in wind speed.	(Dehnhard *et al.*, 2013)
Wind direction	1948	Winds from a westerly direction are linked to enhanced upwelling, and prey availability. Shifts in latitudinal position of westerly wind belt are associated with SAM (Lovenduski and Gruber, 2005). At Macquarie Island, the number of observed days of north-westerly winds has decreased, but the strength of the north to north-westerly wind has increased. This in turn has decreased the number of calm days (Adams, 2009).	Foraging mass gain was linked to westerly winds in *Eudyptes chrysocome*.	(Dehnhard *et al.*, 2013)

Appendix I. Pearson correlation values to colour to visually summarise *Arctocephalus gazella* and *Arctocephalus tropicalis* cohort survival probabilities at Macquarie Island in relation to three independent environmental parameters: sea level pressure, sea surface temperature, and wind speed. Green denotes a higher Pearson correlation value in relation to other values, and *visa-versa* for the colour red. Absence of colour and * symbol denotes the Pearson correlation was not significant. Percentages represent *A. gazella* and *A. tropicalis* cohort survival probability change in relation to a unit increase in each environmental parameters. This equates to 1.0 °C increase in sea surface temperature, 1 hPa sea level pressure and 1 km/h increase in wind speed.

	A. gazella		***A. tropicalis***		
	Pup	**Adult**	**Pup**	**Adult**	**Environmental variables**
Female	-0.2 % (-0.014)	0.2% (0.003)	-2.9% (-0.022)	-0.6% (-0.006)	Sea level pressure (hPa)
	-13.0% (-0.1068)	2.4% (0.005*)	-4.5% (-0.1079)	-4.7% (-0.0169)	Sea surface temperature (°C)
	0.7% (0.007)	1.3% (0.017)	-0.4% (-0.0784)	1.3% (0.015)	Wind speed (km/h)
Male	-1.1% (-0.006)	1.0% (0.011)	-1.1% (-0.014)	0.1% (0.002)	Sea level pressure (hPa)
	-6.1% (-0.075)	3.1% (0.029)	-11.1% (0.0784)	-0.5% (-0.000*)	Sea surface temperature (°C)
	-1.9% (-0.005)	2.5% (0.018)	-0.3% (-0.005)	1.6% (0.014)	Wind speed (km/h)